

## Abstract

YOSHIZAKI, JUN. Use of Natural Tags in Closed Population Capture-Recapture Studies: Modeling Misidentification. (Under the direction of Kenneth H. Pollock and Nicholas M. Haddad.)

Estimates of demographic parameters such as population size, survival rates, and movement rates are often obtained by use of capture-recapture models. Capture-recapture methods usually require the capturing and marking of animals. These marks allow us to identify animals upon their recapture and create unique capture histories for each animal captured. Then, parameter estimates are obtained based on modeling the capture histories. Traditionally, marks or "tags" are applied by researchers (applied tags). However, in recent years, naturally existing features of animals have also been used as tags in capture-recapture studies (natural tags).

Our research focuses on the use of natural tags as an alternative to applied tags in closed population capture-recapture studies. We consider plausible misidentification mechanisms for individual-level natural tags and describe in detail how misidentification leads to errors in the observed capture history data. Effects on the observed capture history data may differ depending on how errors are introduced because the misidentification mechanism may vary depending on the type of natural tag and specific features of the study design. We found that the typical multinomial approach to model capture history data is not applicable when misidentification is possible, and it is important to clearly define the misidentification mechanism in a particular study to model misidentification appropriately.

We first consider misidentification when using genetic tags in closed population capture-recapture studies (non-evolving natural tags 1). We then focus on the use of photographic tags, where two different types of errors are considered: those related to quality of photographs (non-evolving natural tags 2) and those related to changes in natural marks (evolving natural tags). For each type of misidentification mechanism, we develop a new closed population model that is applicable to that specific case and estimators based on quadratic distance functions. The models can be viewed as extensions of the traditional closed capture-recapture model that allows time variation in capture probabilities. Our goal is to present a clear framework for each misidentification mechanism and give its statistical model development. Through simulation studies, we show

that bias in traditional population size estimators can be substantial because misidentification is ignored, and our new estimators perform well in terms of both bias and precision provided capture probability is not too low.

For non-evolving natural tags 1, we also present an alternative estimation method, which is based on likelihood theory, by conditioning on the capture histories that have two or more capture events. With the likelihood-based approach, only part of data can be used, and capture probabilities and misidentification rate cannot be estimated separately. However, population size can be estimated as a derived parameter, and through simulation study, we show that this likelihood-based estimation method is of comparable accuracy to the quadratic methods that use all of the capture history data, except in cases with low capture probabilities where the quadratic distance estimators perform better. We also consider a variation of the basic model in which we allow for behavioral response, but no time variation, with possible misidentification. We show that population size is overestimated when misidentification is ignored, and performance of our new estimators is good provided capture probability is not too low. Finally, we discuss augmentation of capture history data with extra data on the misidentification rate. We particularly consider use of supplemental data obtained when identification is performed multiple times independently (multiple identification), and develop a model that allows us to utilize the augmented data. Although we demonstrate the benefit of the supplemental data for the cases where capture probability is low, in cases where capture probability is high, the benefit of supplemental data is less apparent and requires future investigation.

USE OF NATURAL TAGS  
IN CLOSED POPULATION CAPTURE-RECAPTURE STUDIES:  
MODELING MISIDENTIFICATION

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# Biography

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# Chapter 1

## Use of Natural Tags in Capture-Recapture Studies

### 1.1 Introduction

Estimates of demographic parameters such as population size, survival rates, recruitment rates and movement rates are often obtained by use of capture-recapture models (Williams et al., 2002). Capture-recapture methods usually require the capturing and marking of animals. These marks allow us to identify animals upon their recapture, and create unique capture histories (e.g. [110], [010], etc) for each animal captured. Parameter estimates are obtained based on modeling the capture histories. These parameter estimates are crucial to building sound population dynamics models, and they may be used in scientifically based management of many wildlife and fisheries populations. Capture-recapture models are of many types depending on the study design, and the data structure and parameters of interest may differ among models. In this chapter, we present a very brief overview of different types of capture-recapture models and properties of tags used to mark animals. We then outline issues that arise with use of natural tags in capture-recapture studies, paying particular attention to the issue of misidentification.

### 1.2 Conventional Capture-Recapture Models

Conventional capture-recapture models are either closed or open models. Estimation of population size is the focus of *closed population models*. These models do not allow additions (i.e.,

births or immigrants) or deletions (i.e., deaths or emigrants) of animals from the population during the study so that the population is constant during the whole study. The *2-sample closed population model*, often referred to as the ***Lincoln-Petersen model***, is the simplest capture-recapture model, and this model assumes equal capture probability for all animals in the population on each sampling occasion. The assumption of equal capture probability can be relaxed with *K-sample closed population models* where  $K > 2$ , which allow for varying capture probabilities due to individual heterogeneity, behavioral response, time variation or combinations of these (Otis et al., 1978; Pollock et al., 1990; Williams et al., 2002).

*Open population models* allow additions or deletions of animals from the population during the study. The general ***Jolly-Seber model*** has  $K > 2$  sampling occasions, and population size, survival rates and recruitment rates can be estimated (Jolly, 1965; Seber, 1965, 1982; Williams et al., 2002). The ***Cormack-Jolly-Seber model*** is based on a component of the Jolly-Seber model that focuses on the estimation of survival parameters, and uses the data conditioned on first capture (Cormack, 1964; Lebreton et al., 1992; Williams et al., 2002).

Another class of models comprise the ***tag-return models*** of Brownie et al. (1985), in which tags are usually returned by harvesters. This set of models is related to, but distinct from, the Cormack-Jolly-Seber model with multiple capture events because animals can be recaptured only once, but again the main focus is on the estimation of survival parameters. ***Multistate models***, which can be considered as another extension of Cormack-Jolly-Seber model, have wide applications in capture-recapture and tag-return studies. Under these models we assume that there are groups of animals in different states (e.g., populations in different locations, animals in different status of breeding), and the focus is estimation of parameters that are related to transitions between different states (e.g., movements from location A to location B, changes from breeder to non-breeder) in addition to survival parameters (Arnason, 1972; Hestbeck et al., 1991; Brownie et al., 1993; Schwarz et al., 1993; Williams et al., 2002).

The ***Robust design*** is another important area of capture-recapture modeling, which provides data from both closed and open populations. The robust design has two different types of sampling periods, primary and secondary. Each primary sampling period has a set of secondary sampling periods nested within it, and primary periods have long intervals between them and assume an open population structure, whereas the secondary periods have short intervals between them and assume a closed population structure within each primary period. The robust study design allows

us to: allow for unequal catchability of animals; estimate parameters that cannot be estimated by closed or open population models alone such as temporary emigration; and improve the precision of parameter estimates (Pollock, 1982; Kendall et al., 1997; Williams et al., 2002).

## 1.3 Tags

### 1.3.1 Types of Tags

Different types of marking methods can be used to obtain capture-recapture data, and here a *tag* refers to any feature that can be used to identify individuals or groups of animals. Many of the conventional tags used in capture-recapture studies are applied to animals by investigators, and we refer to them as *applied tags*. Traditionally capture-recapture methods are based on applied tags (Seber, 1982), and there are many different types of tags depending on the animals being studied. Some examples of applied tags include physical devices or modification of the animals, such as numbered bands, radio tags, satellite tags, or tattoos.

In capture-recapture studies, applied tags have many advantages because tags can be designed to suit the purpose of the study, and are in many ways under the researchers' control. On the other hand, there are aspects of applied tags that are not desirable. Of particular concern is the necessity to physically capture animals to apply the tags, which may be very problematic if the species of interest is elusive or expensive to physically capture. Also, physically attaching tags to animals can cause various problems such as discomfort and infection, which can affect survival and capture probability. Further, applied tags may be lost during the study.

On the other hand, naturally existing features of animals (natural marks) can also be used to mark animals, and we refer to tags based on natural marks as *natural tags*. Visible features of animals such as variation in stripe patterns on tigers and scars on manatees (e.g., Pennycuick, 1978; Hammond, 1986; Karanth et al., 2004b; Langtimm et al., 2004) have been widely used as tags by taking their photographs, which we refer to as *photographic tags*, and use of photographic tags has been an important area of capture-recapture research (e.g., Agler, 1992; Bain, 1992; Durban et al., 2005). Recently, advances in technology have opened the use of natural tags to a wider range of ecological studies, and there is now a growing body of literature on the use of different types of natural tags instead of applied tags. For example, techniques developed in forensic science allow

us to use genotypes to mark animals, which we refer to as *genetic tags* (also DNA fingerprints) (Waits, 2004). Such techniques are currently used in many capture-recapture studies (Waits and Paetkau, 2005), and are another important area of capture-recapture research (e.g., Mills et al., 2000; Gosky, 2004; Lukacs, 2005; Lukacs and Burnham, 2005). There are many other types of natural marks that can be used as tags as well (e.g., otolith chemistry), but in our discussion we shall mainly focus on use of photographic tags and use of genetic tags.

Natural tags are less invasive than applied tags because it is often not necessary to physically capture the animals. Therefore, natural tags might appear to be more advantageous in capture-recapture studies. This may be true in some cases, however, there are aspects of using natural tags that lead to new challenges that were not faced when using applied tags. Such new challenges can be summarized into three main issues:

1. uncertainty in the level of identification;
2. misidentification or misclassification; and
3. unmarkable animals.

We are left with the common dilemma in decision making of trade-offs, and to assess these trade-offs, it is necessary to have a very clear framework for the modeling of capture-recapture data based on natural tags and the assumptions involved. In later sections, we will discuss each issue briefly.

### 1.3.2 Level of Identification

It is also important to consider the level of identification that can be achieved by use of the tags. In capture-recapture studies, the necessary level of identification of animals differs depending on the purpose of study. For example, some studies only need to identify groups of animals that share some aspect of their life history in common (e.g., fish from the same natal river) whereas others require identification of individual animals. Tags that only allow us to identify groups of animals that share some aspect in common are referred to as *population-level tags*. Those that allow us to identify each individual animal are referred to as *individual-level tags*. Colored bands, patterns in gene expression and otolith microchemistry are good examples of population-level tags

Table 1.1: A summary of terms used to define types of tags and types of capture histories.

Glossary	
Tags	Any features that can be used to identify animals
Applied tags	Tags that are applied by investigators
Natural tags	Tags based on naturally existing features of animals
Genetic Tags	Example of natural tags; obtained from analyses of DNA samples
Photographic Tags	Example of natural tags; use visible unique feature of animal
Population-level tags	Tags that can be used to identify groups of animals only
Individual-level tags	Tags that can be used to identify individual animals
Non-evolving natural tags	Natural tags that are not likely to change over time
Evolving natural tags	Natural tags that can change over time
True capture history	Capture history that corresponds to capture events, and unknown when there is possible misidentification
Observable capture history	Capture history that can be observed
Real capture history	Capture history that belongs to existing animals and may or may not contain misidentification
Ghost capture history	Capture history that belongs to non-existing animals, and is created by misidentification

whereas individually numbered bands, coloration patterns and genotypes are good examples of individual-level tags. A glossary of terms used is presented here to aid the reader (Table 1.1).

### 1.3.3 Tag-Related Assumptions

There are several underlying assumptions, not always explicitly stated, in capture-recapture studies that are specific to the properties of tags. These are relevant to both applied and natural tags. Conventional capture-recapture models assume that:

1. All captured animals can be tagged in some way;
2. The tags do not affect survival;

3. The tags are not lost or modified during the study;
4. The tags are unique to the level of interest (e.g., population- or individual-level); and
5. The tags allow correct identification of captured animals.

These assumptions plus additional assumptions about capture probabilities are necessary to obtain estimates that are unbiased. Any violation of these assumptions can have serious consequences. Thus, properties of tags are an important aspect of capture-recapture studies, and assumptions that are more or less likely to be violated may differ among different tag types. We shall explore violation of these assumptions in detail as they relate to the use of various types of natural tags in later sections.

### 1.3.4 Special Issues with Natural Tags

Traditionally in capture-recapture studies, investigators assume that the level of identification (i.e., population- or individual-level) is known, and information to identify animals at the level of interest is known with certainty. This is particularly true with applied tags. For example, we know that individually numbered bands can be used to uniquely identify marked individuals and that the identification number that is applied to each captured animal is known with certainty. In other words, we can have a catalog of tags in which the identification information on the tags is known with certainty. However, natural tags often do not allow us to have identification information that is certain. For example, a catalog of each captured animal's genotype (i.e., DNA fingerprints) may be obtained by analyzing the DNA sample upon capture events. Two problems with identification are possible here: the genotype may not contain enough information to distinguish each animal in the population (Mills et al., 2000; Gosky, 2004), and the DNA fingerprint may contain errors due to faulty field or laboratory work (Lukacs and Burnham, 2005). The former problem causes the situation in which multiple animals share the same genotype, thus the tag should not be used for individual identification (*uncertainty in the level of identification*). The latter problem causes the situation that the tag information is incorrect, thus it can lead to incorrect identification of individual animals when tags are used at the individual-level (*misidentification*), or to incorrect status when tags are used at the population-level (*misclassification*).

These are new challenges we have with natural tags, and the resulting violations of the assumptions of conventional capture-recapture models may lead to large biases in parameter estimates. In the next section, we focus on use of individual-level natural tags, and explore potential violations of conventional capture-recapture model assumptions and their effects on capture-recapture data in general.

## 1.4 Individual-Level Natural Tags

### 1.4.1 Overview

There are many types of natural marks of animals that can be used to mark individual animals, however, individual-level natural tags can be classified into two main categories: genetic tags and photographic tags. We will focus closely on these two types of individual-level natural tags to illustrate potential issues. Genetic tag-based capture-recapture studies typically involve collection of physical material in the field (e.g., blood, skin or hair) that contains the animal's DNA, extraction of DNA, and amplification of the DNA to obtain "DNA fingerprints" (or genetic tags) using a technique called polymerase chain reaction (PCR). Each captured individual can then be identified based on the DNA fingerprint (Waits, 2004), which allows us to construct capture histories of animals in the population.

The second type of study uses unique visible features of animals, and there are many variations in natural marks that can be used (e.g., coloration patterns and injury scars). These studies often employ a photographic identification technique, which typically involves taking photographs of the natural marks in the field. Then, identification is performed based on the photographic records of natural marks (photographic tags) (Karanth et al., 2004a). Matching of newly photographed natural marks to the ones in photographs from previous sampling occasions indicates a recapture event, while non-matching indicates a first capture event. In some cases and particularly with terrestrial species, sampling is automated by setting camera traps in the fields (e.g., tigers in Karanth, 1995). In other cases, and particularly with highly visible aquatic species such as marine mammals, photographs are taken based upon visual encounters during field surveys (e.g., manatees in Langtimm et al., 2004). The brief summary of types of natural tags is shown in Figure 1.1.

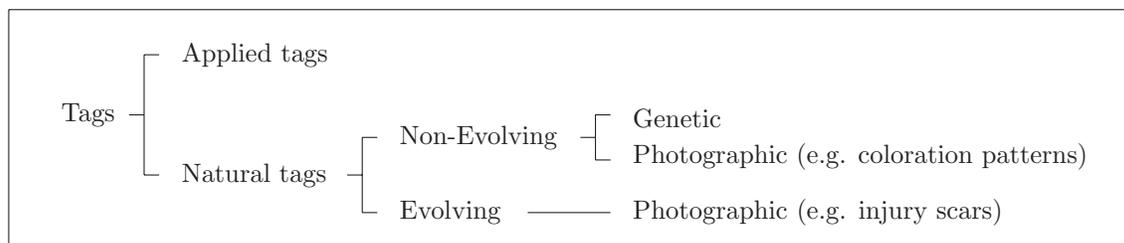


Figure 1.1: A summary diagram of tag types commonly used in capture-recapture studies.

## 1.4.2 Potential Assumption Violations

### Misidentification

Theoretically, genetic tags possess good properties as a tag in capture-recapture studies because:

- all animals can be tagged;
- the tag is unique to an individual animal; and
- there is no loss or modification of the tag.

However, there are a number of potential problems associated with use of this method in practice. The quality of the samples, which can be affected by field techniques and storing methods, can cause errors in the DNA fingerprints. Also, errors in DNA fingerprints can be introduced in the laboratory (Taberlet et al., 1999; Waits, 2004; Waits and Paetkau, 2005). If the DNA fingerprints contain errors for any reason, they lead to incorrect identification of individual animals (violation of assumption 5).

Similarly, misidentification of animals is possible with photographic tag-based studies, which can be caused by a number of factors. For example, less distinctive natural marks or poor quality photographs may increase the risk of errors during the process of matching photographs. In addition, unlike genetic tags, some visible natural marks are not consistent over time, for example, scars are subject to loss or modification over time (e.g., Carlson et al., 1990), possibly making the misidentification issue more complicated (violation of assumption 3).

Whether a certain type of natural tag can be lost or modified over time is an important aspect of misidentification, and here we make a division of natural tags into two different types.

We refer to natural tags that are not likely to change over time as *non-evolving natural tags*, and those that can change over time as *evolving natural tags*. For example, it is reasonable to consider that genetic tags and photographic tags that use coloration patterns like stripes on tigers are non-evolving natural tags, but photographic tags that use injury scars on species like manatee are evolving natural tags in long-term studies. However, whether a certain type of natural tag is non-evolving or evolving needs to be justified for each study based on considerations such as the specific natural tag involved, the sampling design, and the duration of study.

Note that minimization of such errors should be an important goal of any study, and there has been research on field and laboratory techniques to minimize genotyping errors (Waits and Paetkau, 2005; Taberlet and Luikart, 1999) and on methods to quantify the magnitude of errors in DNA fingerprints (Bonin et al., 2004; McKelvey and Schwartz, 2004; Buchan et al., 2005). For studies that use photographic tags, there are now detailed protocols to avoid mismatching of photographs (e.g., Defran et al., 1990), and computer programs have been developed to aid the matching process (e.g., Arzoumanian et al., 2005). However, misidentification may never be eliminated completely. Thus, in addition to the effort to minimize errors that lead to misidentification, it is important to develop models that allow misidentification in order to analyze natural tag-based capture-recapture data.

### Uncertainty in the level of identification

Another potential challenge is uncertainty in the level of identification (violation of assumption 4). For example, in genetic tag-based capture-recapture studies, the genotype would not provide enough information to identify individuals if the number of loci examined is too small, leading to a situation in which a number of individuals share the same genotype (Taberlet and Luikart, 1999; Waits, 2004). Thus, it would be only possible to identify groups of individuals within the population. In such cases, genotype should be treated as a population-level tag, but information such as the number of distinct genotypes in the population and the number of animals that share each genotype is unknown, and thus need to be estimated. This problem is often referred to as the *shadow effect*, and data should be analyzed with a model that incorporates such uncertainty (Mills et al., 2000; Gosky, 2004) (see also Figure 1.2).

Uncertainty in level of identification can also be a problem in photographic tag-based studies.

For example, there may be animals that possess similar injury scars, making them difficult to distinguish. Therefore, we cannot be absolutely sure that these natural marks are unique to each animal (Pennycuick, 1978). This problem should be avoided by carefully choosing which natural marks should be used in the study or by using multiple natural marks for identification so that animals are identified correctly to the level of the investigators' interests and needs.

### Unmarkable animals

In photographic tag-based studies, it may be the case that we have *unmarkable animals* (violation of assumption 1). For example, there may be animals that do not possess distinct injury scars or young animals in which natural marks have not yet fully developed. Unmarkable animals cannot be followed to construct their capture histories due to lack of identifiable natural marks, and the only data we can obtain from them are total number of photographs taken at each sampling occasion. Consequently, if data on unmarkable animals are ignored, estimates are only applicable to the markable portion of the population, similar to the case of uncachable animals for a particular trapping method (Seber, 1982). In some studies, unmarkable animals are a serious problem, for example, the majority ( $\approx 70\%$ ) is considered as unmarkable in bowhead whale populations, and special capture-recapture models that incorporate unmarkable animals have been developed (Da Silva et al., 2000, 2003).

### 1.4.3 Modeling Misidentification

Although misidentification can occur with applied tags (e.g., as when numbers on leg bands are misread), the potential for misidentification is greater and a more serious problem when natural tags are used in capture-recapture studies. It is important to remember that there is always a risk of misidentification with individual-level natural tag-based capture-recapture studies. Such data should be analyzed using models in which an appropriate misidentification mechanism for the data is incorporated. However, it is often difficult to identify the appropriate misidentification mechanism, and here we give a simple example of a capture-recapture study to illustrate necessary considerations and the effects of misidentification on observed capture-recapture data.

**Who is identified through misidentification?**

Consider a single sampling occasion. Suppose an animal A is captured. Then, identification of animal A can be either correct or incorrect. If identification of the animal was incorrect, then the question is whose identity is assigned to animal A. In some cases correct identification of marked animals may not be possible even with applied tags, for example, if the last digit of the identification number on the tag is lost. However unless the tags are completely lost, investigators can identify the problematic tags because they know the identification numbers applied to previously captured animals. Thus, this type of misidentification can be removed from capture-recapture data when applied tags are used. There are other situations where misidentification of applied tags occurs but is not recognized, for example, when tags are read from a distance and misidentified as another tag. In such cases, incorrect identification always leads to false identification of other animals in the population that have already been captured. Schwarz and Stobo (1999) termed this problem *tag-misread*, investigated its effect in capture-recapture studies, and developed models to estimate tag-misreading rates.

On the other hand, with natural tags, it is not known when an identification error has occurred, and misidentification cannot be restricted to cases that lead to false identification of existing previously marked animals in the population. In other words, misidentification of an animal can lead to two types of error: (1) assigning the identity of an animal in the population to a different animal, and (2) assigning an identity that does not exist to a new capture or to a recaptured animal. The consequences of misidentification in capture-recapture data differ depending on the assumptions made concerning the mechanisms of misidentification. For example, assigning the identity of a previously tagged animal to an existing animal in the population results in the combining of capture histories of two animals, whereas assigning a non-existing identity to a captured animal results in splitting of the capture history of an animal into multiple capture histories.

Theoretically, any type of misidentification can occur with natural tags. However considering all possible ways that errors in identification can be introduced, there are numerous different effects of misidentification on the observed capture history data, and hence on parameter estimates from traditional models that assume no misidentification. We believe that it is not practical to consider all possible scenarios and incorporate them into capture-recapture models. Thus, it is important

to identify the mechanisms of misidentification that are most likely to occur in the study, make appropriate assumptions, and develop models based on the assumptions. For example, Lukacs and Burnham (2005) studied the particular case of misidentification when genetic tags are used. They assumed that misidentification leads only to creation of non-existing animals based on the fact that the number of possible genotypes greatly exceeds the number of individuals in the population, and that errors in a DNA fingerprint are unlikely to generate a fingerprint that matches that of another existing animal in the population. This assumption seems to be reasonable for the case of genetic tags, and it also helps to simplify the issue of misidentification.

### **When can misidentification occur?**

Another aspect that needs to be considered is whether misidentification is possible at all sampling occasions or not. Identification errors in photographic tag-based studies are likely to be due to matching errors when newly taken photographs are compared to previously taken photographs, and therefore may not apply to the first capture event. However with certain types of natural tags, we should include the possibility of misidentification when animals are captured for the first time. For example, the likelihood of errors in DNA fingerprints does not depend on whether the animal is a first-time capture or a recapture, and misidentification can occur at both first capture and recapture events. Consequently, it is again important to consider how errors in identification can be introduced during the study to model misidentification appropriately.

### **Can errors be repeated?**

It is also important to consider whether the same identification error can occur more than once during the study. Theoretically, the same false identity can be created on one or more sampling occasions for the same animal or for multiple different animals. The resulting effects on capture-recapture data differ depending on how repeated errors can occur during the study. The simplest case is to assume that an error is never repeated, and we term this situation as *unique identification errors*. This may be an oversimplification, but may be necessary to keep models parsimonious and useful for estimation.

### Effects of misidentification on observed capture-recapture data

To illustrate the effects of misidentification on observed capture-recapture data, and consequences for modeling such data in general, we use a simple example assuming that misidentification always leads to a non-existing animal, misidentification can occur at any sampling occasion and identification errors are unique. Consider a 2-sample capture-recapture study and an animal that was captured on both occasions. This animal has a *true* capture history [11] where true capture histories are the ones that correspond to the capture events. The true capture histories may or may not agree with the observed capture histories (i.e., data) when misidentification is possible, and they agree with observed capture histories only if identification is correct at all captured events.

Suppose the animal was identified correctly on the first capture, but misidentified at the second capture. Then, the capture history of the animal at the second sampling occasion is recorded as non-capture (i.e., [0]), and the capture event is recorded as a first capture for a non-existent animal, generating two histories, [10] and [01], for the same animal. We refer to capture histories that belong to existing animals, whether or not they contain misidentification, as *real* capture histories, whereas those that belong to non-existing animals as *ghost* capture histories. Note that, for this model, on subsequent sampling occasions, the animal is again subject to capture, and the real capture history can include future recaptures. However, the ghost capture history cannot include recaptures because we assume that the ghost capture history belongs to a non-existing animal and the error that led to the non-existing animal is never repeated.

This type of misidentification has unique consequences for the observed capture histories. For an animal identified correctly at sample 1 and misidentified at sample 2, two capture histories [10] and [01] are generated with the second history being a ghost capture history as defined above. The probability, with which the ghost history occurs, can be determined based on the misidentification mechanism we assume. These two paired histories for one animal are created by a single event, thus they are not independent. In other words, conditional on [11] being the true capture history and there being one misidentification at the second occasion, we have two totally dependent capture histories with the same probability. Of course the observed histories [10] and [01] can arise in other ways as well, based on other capture and misidentification events, and we can create a list of *observable* capture histories for each true capture history. However, obviously, they are also not independent histories, and we cannot distinguish real and ghost capture histories in the observed

data. Hence the recorded capture histories do not represent independent fates of the  $N$  animals in the population and the usual multinomial distribution does not apply.

To summarize, the problem here is that, under specific assumptions, the capture history of an animal can split into multiple capture histories when misidentification occurs, and the "real" capture history with incorrect identification and its "ghost" capture history are always observed together, but as if they were different animals. This unique characteristic of the observed capture histories has very serious consequences. "Fates" are not independent, and the sum of the marginal probabilities of all the possible capture histories exceeds 1 because of the ghost capture histories. Consequently, the counts of observed capture histories cannot be modeled with the multinomial distribution involving population size  $N$  as is the case of conventional closed population capture-recapture models. Estimates are likely biased if this type of capture history data is analyzed by conventional capture-recapture models. The key to this problem is to understand the misidentification mechanism that is likely to occur in the study, and construct a list of observable capture histories and their probabilities based on assumptions that are appropriate for the specific misidentification mechanism.

## 1.5 Population-Level Natural Tags

In the previous section, we noted that many natural tags are suitable for individual identification of animals, and discussed potential issues with use of individual-level natural tags in capture-recapture studies. Some natural tags only allow identification to the population level (i.e., a group of individuals that share an aspect in common), and with population-level natural tags, the potential assumption violations discussed for individual-level natural tags also need to be considered. For example, a set of trace elements in the otolith of a fish (Thorrold et al., 1997) is a type of population-level natural tag. Analyses of trace elements provide a signature which enables a fisheries scientist to identify where the fish was born or where the fish was at a later age (*state*) and construct the history of locations where the fish has been (*transition history*), thus enabling the researchers to gain information on age-related movement probabilities (C. Jones, personal communication). Similar to misidentification issues discussed in the previous section, there is always a risk of errors in identification of state when natural tags are used (*misclassification*), and observed transition histories do not necessarily correspond to the true transition histories. For

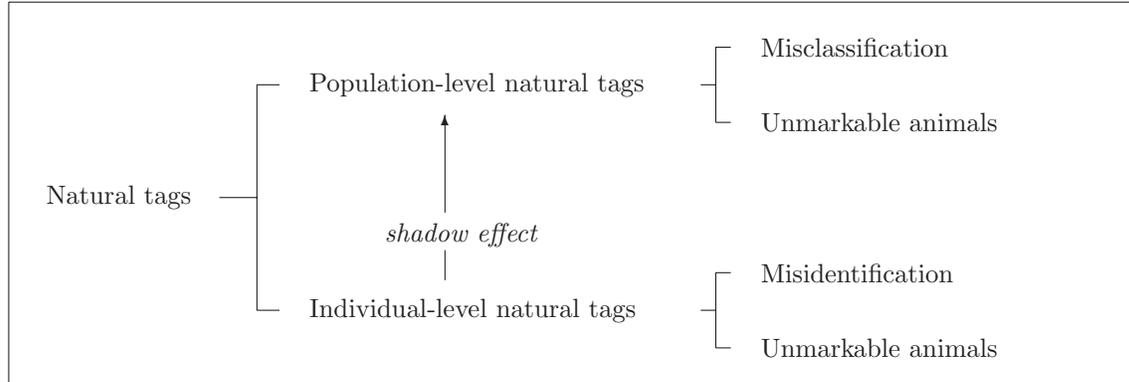


Figure 1.2: A summary diagram of issues with use of natural tags in capture-recapture studies.

example, identification of locations of the fish based on the trace element may contain errors, thus the observed history of locations may not correspond to the history of locations where the fish has been. It is again necessary to consider the mechanism of misclassification and its effects on the observed data so that appropriate models for the data can be developed.

## 1.6 Discussion

In summary, the use of natural tags can create problems that do not occur when using applied tags (Figure 1.2). There is always uncertainty associated with identification based on natural tags, and misidentification or misclassification is always a risk. In addition, issues with natural marks can be complex depending on the type of natural tags used in the study. For example, injury scars may change over time, and thus the misidentification issue can be more complex, or coloration patterns may not be established until a certain age class has been reached, and thus young animals are unmarkable. Although we have not emphasized the issue of unmarkable animals in this chapter, it is also an important issue. The potential for errors in identification clearly raises questions in data analyses. Analyses using conventional capture-recapture models may not be appropriate, and special models need to be developed that account for these special challenges.

Particular attention has been paid to the issue of misidentification in capture-recapture studies, which can be very complex depending on the assumptions we make about the way errors in identification are introduced. Underlying mechanisms of misidentification, and hence the assumptions

we make, can differ depending on study species, tag types, study design, etc., and understanding the mechanisms is very important to appropriately model the misidentification process. In the following three chapters, we consider plausible misidentification mechanisms for individual-level natural tags and new models that are applicable to such cases. Our goal here is to present a clear framework for the misidentification mechanism, and with the development of new models, we take a stepwise approach starting with simpler cases first. For all models, we assume that the population is closed during the period of the study. In Chapter 2, we develop a basic closed population model that can be applied to genetic tag-based capture-recapture data. In Chapter 3, we consider an alternative estimation approach for the data described in Chapter 2 that is based on a conditional likelihood, and also extensions of the model presented in Chapter 2 by including behavioral responses and augmentations of data that provide extra information on the misidentification rate. In Chapter 4, we focus on misidentification issues in photographic tag-based capture-recapture studies, and develop new models for these studies.

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## Chapter 2

# Non-Evolving Natural Tags 1: Possible Misidentification at Any Capture

### 2.1 Introduction

Individual identification based on an individual animal's genotype (*genetic tag*) has become an important tool in ecological studies (Waits, 2004). Typical genetic tag-based capture-recapture studies involve collection in the field of samples that contain an animal's DNA, followed by analyses of the DNA samples in the laboratory to obtain genetic information. These analyses involve extraction of DNA from the material and amplification of DNA (Taberlet and Luikart, 1999; Waits, 2004). The resulting "DNA fingerprints" (or genetic tags) are used for individual identification, and capture-recapture data can be constructed based on the individual identification. There are different types of genetic material that can be collected as a source of DNA in the field, for example, hair for brown bears (*Ursus americanus*) (Woods et al., 1999), skin tissue for humpback whales (*Megaptera novaeangliae*) (Garrigue et al., 2004), and fecal samples for common wombat (*Vombatus ursinus*) (Banks et al., 2002). The number of genetic tag-based capture-recapture studies has increased recently (Lukacs and Burnham, 2005*b*), and the method has been applied to at least 13 different species to obtain minimum count or capture-recapture estimates of population size (Waits and Paetkau, 2005).

Use of genetic tags in capture-recapture studies is attractive, especially for rare or elusive

species, because, in some cases, capture-recapture data can be obtained without physically contacting or even observing the animals, and theoretically genetic tags produce unique individual-level tags. However, there are always technical challenges, such as risk of contamination, amplification failure, and genotyping errors, and this method does have practical problems (Taberlet et al., 1999; Taberlet and Luikart, 1999; Waits, 2004). One of the important issues is the uncertainty in level of identification, which is often referred as to the *shadow effect*. This is the situation where multiple animals share the same genotype due to the DNA fingerprints being based on an insufficient number of loci, and it leads to underestimation of population size (Mills et al., 2000; Waits, 2004). Another important issue is errors in DNA fingerprints, which can lead to misidentification of individual animals, and capture-recapture data that contain errors due to misidentification lead to overestimation of population size (Waits, 2004). Such bias in the population size estimates can be substantial, for example, misidentification could lead to a 5.5-fold increase in estimated population size in the case of Yellowstone wolves (*Canis lupus*) if unaccounted for in the capture-recapture model (Creel et al., 2003).

There are now several studies available in the literature that examine the solutions to these issues, many of which are related to field methods and laboratory techniques, which include guidelines for pilot studies to examine the feasibility of the use of DNA samples (Taberlet et al., 1999; Valiere et al., 2007), precautions and protocols for analyses of samples (Taberlet and Luikart, 1999; Paetkau, 2003; Waits and Paetkau, 2005), methods to compute the proportion of the population that have indistinguishable genotypes (Waits et al., 2001), and methods to detect and quantify the magnitude of genotyping errors (Bonin et al., 2004; McKelvey and Schwartz, 2004; Buchan et al., 2005). However, less attention has been paid to the modeling of genetic tag-based data within the capture-recapture framework (Lukacs and Burnham, 2005b). It would be ideal if errors in DNA fingerprints could be eliminated through careful methodological and technical considerations. However, there are many factors that may cause such errors, and it is often very difficult and expensive to eliminate them. Thus, it is beneficial to have models that allow for errors in capture-recapture data. Gosky (2004) considered the issue of the shadow effect and developed capture-recapture models that can be applied to data that have the shadow effect. Recently, Lukacs and Burnham (2005a) considered cases of misidentification that are likely to occur in genetic tag-based capture-recapture studies and presented a model that attempts to incorporate misidentification.

In this chapter, we will not focus on field and laboratory techniques to minimize misiden-

tification from genetic tag-based capture-recapture data, although we do recommend this as an important area for research. Instead, we shall assume that, even in well designed genetic tag-based capture-recapture studies, the data always have a risk of containing errors due to misidentification, and we will develop a framework for misidentification mechanisms that are likely to occur in genetic tag-based capture-recapture studies and then develop a statistical model that can be used to analyze such data. We consider studies where the population can be assumed to be closed, and our assumptions are similar to the assumptions of Lukacs and Burnham (2005a): however our model formulation and hence the resulting estimates are quite different from theirs.

## 2.2 Lukacs and Burnham Misidentification Model

Lukacs and Burnham (2005a) considered misidentification when an animal's genotype is used as an identification tool in closed population capture-recapture studies. They assumed that:

1. The genotype is unique to each animal if correctly identified;
2. A genotyping error always leads to a genotype that is not identical to that of any animal in the population; and
3. Two errors made at different sampling occasions never produce the same (incorrect) genotype.

Assumption 1 implies that the genetic tag is an individual-level tag. Assumption 2 implies that misidentification always leads to identification of a non-existing genotype or "ghost", and the possibility of recapture of the non-existing genotype is eliminated by assumption 3. Consequently, with their closed population model, recorded capture histories that have only one capture event can contain misidentification, whereas recorded histories containing at least one recapture cannot involve any misidentification. In addition, though not explicitly stated, their multinomial likelihood also implicitly assume that

4. The non-existing genotypes are present in the population from the beginning of the study, and existing and "non-existing" genotypes suffer independent outcomes.

In other words, their likelihood considers a population of genotypes rather than a population of animals, and non-existing genotypes are subject to capture during the study, but they can only

be captured once. We shall see later that this final assumption is not required in our alternative model formulation.

Lukacs and Burnham (2005a) give the probability of observing each capture history  $h$  in a  $K$ -sample study as:

$$\Pr [h] = \left[ \prod_{i=1}^{t_1-1} (1 - p_i) \right] [p_{t_1} \alpha] \left[ \prod_{i=t_1+1}^K c_i^{h_i} (1 - c_i)^{1-h_i} \right]$$

for  $h$  with multiple capture events, and

$$\Pr [h] = \left[ \prod_{i=1}^{t_1-1} (1 - p_i) \right] \left[ p_{t_1} \alpha \left( \prod_{i=t_1+1}^K (1 - c_i) \right) + p_{t_1} (1 - \alpha) \right]$$

for  $h$  with a single capture event at sample occasion  $t_1$ , where

- $t_1$  is the time that the genotype is initially observed
- $h_i$  is the  $i$ th entry of capture history  $h$
- $p_i$  is the probability of initially observing a genotype at time  $i$
- $c_i$  is the probability of subsequently observing (i.e., recapturing) a genotype at time  $i$
- $\alpha$  is the probability of correctly identifying a genotype given that it is observed for the first time.

Based on the assumptions, and the above probabilities, they constructed the full multinomial likelihood (omitting constant terms) as

$$\mathcal{L}(f_0, p_i, c_i, \alpha | n_h, M_{t+1}) \propto \frac{(f_0 + M_{t+1})!}{f_0!} \prod_h \Pr [h]^{n_h},$$

where

- $f_0$  is the number of genotypes in the population that are never observed
- $n_h$  is a count of the number of times capture history  $h$  is observed

$M_{t+1}$  is the number of distinct genotypes observed,

and estimates are obtained by maximizing  $\mathcal{L}$ . Note that the population size,  $N$ , is not in their likelihood specification. It is estimated as a derived parameter based on estimated  $f_0$  and  $\alpha$  as

$$\hat{N} = \hat{\alpha} \left( \hat{f}_0 + M_{t+1} \right).$$

Assumption 4 of Lukacs and Burnham (2005a) does not seem correct to us, one reason being that the fates of a ghost and the corresponding existing animal are not independent. Therefore we were not satisfied with their approach and decided to take a more basic approach to modeling the capture history data obtained under this type of misidentification.

## 2.3 Proposed Misidentification Mechanism

We made the same basic three assumptions concerning the misidentification process as do Lukacs and Burnham (2005a). Thus, we assume:

1. Misidentification of animals always leads to false identification of animals that do not exist in the population;
2. The same error is never repeated; and
3. Misidentification can occur at any capture event.

Assumption 3 implies that errors in identification information are possible at any sampling occasion whenever animals are captured. For example, errors in identification of applied tags are unlikely to occur when an animal is captured for the first time unless information on the tag is recorded incorrectly. However, genotyping errors are possible whenever DNA samples are analyzed to obtain information about the genotypes (i.e., DNA fingerprints). In other words, the possibility of errors in the DNA fingerprint, and thus misidentification of the animal, does not differ whether the animal is captured for the first time or recaptured. Unlike Lukacs and Burnham (2005a), we do not assume that the non-existing genotypes are present from the beginning of the study, nor that fates of existing and non-existing genotypes are independent. Instead, we assume that each misidentification creates a pair of histories, a real history and a ghost history, which therefore have the same probability of occurrence.

Although we consider genetic tags throughout this chapter, our methods apply to any natural tags that have this type of misidentification mechanism, which we refer to as *non-evolving natural tags 1*. We denote the model developed for capture-recapture data with this type of misidentification as *NE1*.

These assumptions combined together allow us to have a simple misidentification mechanism with the following characteristics:

- Misidentification can occur at any sampling occasion whenever an animal is captured;
- If a captured animal is incorrectly identified, the capture event of that animal appears as a non-capture (i.e., the "real" capture history is recorded as  $[0]$ ), but it also creates a capture history of a non-existing animal (i.e., a "ghost" capture history is created by recording the capture event  $[1]$  for the sampling occasion); and
- The real capture history has a possibility of recapture in the future whereas the capture history of the ghost cannot contain a recapture.

Unlike Lukacs and Burnham (2005a), we assume that non-existing genotypes do not occur until misidentification creates them, and outcomes of existing animals and their "ghost" counterparts are not treated as independent. We will see that this has very serious implications for the statistical model that we develop in the next section.

## 2.4 Statistical Model Development

### 2.4.1 Model Formulation and Simple Examples

We now formalize our earlier heuristic development of the misidentification mechanism. To consider misidentification in a statistical modeling framework, it is helpful to consider capture histories in terms of the *true* capture history (which is unknown with natural tags) vs. the *observable* capture history (which is the list of capture histories that can be observed as data). The true capture history, which is denoted by  $\omega$ , describes the sequence of capture and non-capture events of an animal during the study. The corresponding random variable is denoted by  $Y_\omega$ , which is the number of animals that have true capture history  $\omega$ . On the other hand, the observable capture history is the history we observe, which is denoted by  $\gamma$ , and the corresponding random variable,

Table 2.1: A summary of notation used for misidentification models.

Notation	
$N$	Population size
$\omega$	True capture history ; $Y_\omega$ = Number of animals that have true capture history $\omega$
$\gamma$	Observable capture history ; $X_\gamma$ = Number of capture histories observed as $\gamma$
$\delta$	Latent capture history ; $Z_\delta$ = Number with latent capture history $\delta$
$p_i$	Probability of capturing an animal at the $i$ th sampling occasion
$q_i$	Probability of not capturing an animal at the $i$ th sampling occasion ; $q_i = (1 - p_i)$
$\alpha, \beta$	Probability of correct identification of a captured animal
$P'_i$	Probability of observing an animal with correct identification ; $P'_i = p_i \alpha$
$Q'_i$	Probability of not observing an animal with correct identification
$t_1(\gamma)$	Sampling occasion at which the first capture event occurs for a give capture history $\gamma$
$t_2(\gamma)$	Sampling occasion at which the last capture event occurs for a give capture history $\gamma$

$X_\gamma$ , denotes the number of capture histories  $\gamma$  observed. Notice that random variable  $Y_\omega$  describes the number of animals, whereas random variable  $X_\gamma$  describes the number of observed capture histories. Without the possibility of misidentification, the observed capture histories always agree with the true capture histories, thus  $Y_\omega = X_\gamma$ . For example, capture history [11] can only be observed if the animal is encountered and correctly identified at samples 1 and 2, hence the observed number of histories [11] must equal the number of animals with true capture history [11], and  $Y_{11} = X_{11}$ . However, with misidentification possible, the observed capture history may or may not agree with the true capture history: they agree only if identifications at all capture events are correct. Terms and notation are defined in Tables 1.1 and 2.1.

To give a simple concrete example, we assume that the population is closed during the period of the study, and consider the 3-sample case with equal capture probabilities except for time variation, which is an extension of Model  $M_t$ . As for the case of a conventional short-term capture-recapture study, we have a parameter for capture probability of an animal at each sampling occasion,  $p_1$ ,  $p_2$  and  $p_3$ . Also assuming that the probability of correct identification is constant for all animals

throughout the study, let  $\alpha$  be the probability of correct identification for a captured animal. (A more general model would allow time dependent  $\alpha$ , however, it would be of little use as we could not estimate time dependent  $\alpha$ ). Consider an animal which is captured at all sampling occasions. The animal has true capture history [111], but there are several possible observed capture histories depending on when misidentification occurs. One of the several possibilities is the pair [101 ; 010], which is the case that identification at first and third capture events is correct, but at second capture event is incorrect. Given that an animal has true capture history [111], the probability of observing the animal with real capture history [101] is  $p_1\alpha p_2(1 - \alpha)p_3\alpha$ . The ghost capture history [010] that is created due to misidentification at the second capture event also has the same probability  $p_1\alpha p_2(1 - \alpha)p_3\alpha$  because real and ghost capture histories are totally dependent. In a similar way, we can list every possible observable history and obtain its probability. Table 2.2 presents the probability of all the observable capture histories conditioned on the true capture history for the 3-sample case. The marginal probabilities for the observed capture histories in the 3-sample case are also summarized in Table 2.3, where  $P'_i = p_i\alpha$  and  $Q'_i = (1 - P'_i)$ . Notice that the total probability exceeds 1 because of the ghost capture histories we observe, and the total probability equals 1 if and only if no misidentification occurs (i.e.,  $\alpha = 1$ ).

For  $K > 3$  the same principles apply. As indicated in the previous section, pairs of real and ghost capture histories are generated if misidentification occurs. Ghost capture histories occur only as capture histories with a single capture event, however, it is not possible to tell whether a capture history observed with a single capture event corresponds to a real animal or a ghost. Let  $t_1(\gamma)$  be the sampling occasion when the first capture occurs for a given capture history  $\gamma$ . Then, the general expression for the probability of observing a capture history  $\gamma$  is

$$\Pr[\gamma] = \prod_{i=1}^K P'_i{}^{\gamma_i} (1 - P'_i)^{(1-\gamma_i)}$$

for  $\gamma$  with multiple capture events, and

$$\Pr[\gamma] = \prod_{i=1}^K P'_i{}^{\gamma_i} (1 - P'_i)^{(1-\gamma_i)} + p_{t_1(\gamma)} (1 - \alpha)$$

for  $\gamma$  with a single capture event, where

Table 2.2: A summary of the observable capture histories,  $\gamma$ , and associated probabilities for non-evolving natural tags 1 for the 3-sample case.

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma   \omega]$
111	none	111	real	$p_1\alpha p_2\alpha p_3\alpha$
		110	real	$p_1\alpha p_2\alpha p_3(1-\alpha)$
	at third	001	ghost*	$p_1\alpha p_2\alpha p_3(1-\alpha)$
		101	real	$p_1\alpha p_2(1-\alpha)p_3\alpha$
		010	ghost*	$p_1\alpha p_2(1-\alpha)p_3\alpha$
		011	real	$p_1(1-\alpha)p_2\alpha p_3\alpha$
	at first	100	ghost*	$p_1(1-\alpha)p_2\alpha p_3\alpha$
		100	real	$p_1\alpha p_2(1-\alpha)p_3(1-\alpha)$
		010	ghost*	$p_1\alpha p_2(1-\alpha)p_3(1-\alpha)$
		001	ghost*	$p_1\alpha p_2(1-\alpha)p_3(1-\alpha)$
	at second and third	010	real	$p_1(1-\alpha)p_2\alpha p_3(1-\alpha)$
		100	ghost*	$p_1(1-\alpha)p_2\alpha p_3(1-\alpha)$
		001	ghost*	$p_1(1-\alpha)p_2\alpha p_3(1-\alpha)$
		001	ghost*	$p_1(1-\alpha)p_2\alpha p_3(1-\alpha)$
	at first and third	001	real	$p_1(1-\alpha)p_2(1-\alpha)p_3\alpha$
		100	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3\alpha$
		010	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3\alpha$
		001	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3\alpha$
	at first and second	000	real	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$
		100	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$
010		ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
001		ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
at first, second and third	000	real	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
	100	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
	010	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
	001	ghost*	$p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)$	
110	none	110	real	$p_1\alpha p_2\alpha(1-p_3)$
		100	real	$p_1\alpha p_2(1-\alpha)(1-p_3)$
	at second	010	ghost*	$p_1\alpha p_2(1-\alpha)(1-p_3)$
		010	real	$p_1(1-\alpha)p_2\alpha(1-p_3)$
	at first	100	ghost*	$p_1(1-\alpha)p_2\alpha(1-p_3)$
		000	real	$p_1(1-\alpha)p_2(1-\alpha)(1-p_3)$
	at first and second	100	ghost*	$p_1(1-\alpha)p_2(1-\alpha)(1-p_3)$
		010	ghost*	$p_1(1-\alpha)p_2(1-\alpha)(1-p_3)$
		010	ghost*	$p_1(1-\alpha)p_2(1-\alpha)(1-p_3)$

Table 2.2 (continued.)

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma \mid \omega]$
101	none	101	real	$p_1\alpha(1-p_2)p_3\alpha$
	at second	100	real	$p_1\alpha(1-p_2)p_3(1-\alpha)$
		001	ghost*	$p_1\alpha(1-p_2)p_3(1-\alpha)$
	at first	001	real	$p_1(1-\alpha)(1-p_2)p_3\alpha$
		100	ghost*	$p_1(1-\alpha)(1-p_2)p_3\alpha$
	at first and second	000	real	$p_1(1-\alpha)(1-p_2)p_3(1-\alpha)$
		100	ghost*	$p_1(1-\alpha)(1-p_2)p_3(1-\alpha)$
		001	ghost*	$p_1(1-\alpha)(1-p_2)p_3(1-\alpha)$
	100	at none	100	real
at first		000	real	$p_1(1-\alpha)(1-p_2)(1-p_3)$
		100	ghost*	$p_1(1-\alpha)(1-p_2)(1-p_3)$
011	none	011	real	$(1-p_1)p_2\alpha p_3\alpha$
	at third	010	real	$(1-p_1)p_2\alpha p_3(1-\alpha)$
		001	ghost*	$(1-p_1)p_2\alpha p_3(1-\alpha)$
	at second	001	real	$(1-p_1)p_2(1-\alpha)p_3\alpha$
		010	ghost*	$(1-p_1)p_2(1-\alpha)p_3\alpha$
	at second and third	000	real	$(1-p_1)p_2(1-\alpha)p_3(1-\alpha)$
		010	ghost*	$(1-p_1)p_2(1-\alpha)p_3(1-\alpha)$
		001	ghost*	$(1-p_1)p_2(1-\alpha)p_3(1-\alpha)$
	010	none	010	real
at second		000	real	$(1-p_1)p_2(1-\alpha)(1-p_3)$
		010	ghost*	$(1-p_1)p_2(1-\alpha)(1-p_3)$
001	none	001	real	$(1-p_1)(1-p_2)p_3\alpha$
	at third	000	real	$(1-p_1)(1-p_2)p_3(1-\alpha)$
		001	ghost*	$(1-p_1)(1-p_2)p_3(1-\alpha)$
000	none	000	real	$(1-p_1)(1-p_2)(1-p_3)$

Table 2.3: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for non-evolving natural tags 1 in a 3-sample study.

$\gamma$ (observed history)	$\Pr[\gamma]$
111	$P'_1 P'_2 P'_3$
110	$P'_1 P'_2 Q'_3$
101	$P'_1 Q'_2 P'_3$
100	$P'_1 Q'_2 Q'_3 + p_1(1 - \alpha)$
011	$Q'_1 P'_2 P'_3$
010	$Q'_1 P'_2 Q'_3 + p_2(1 - \alpha)$
001	$Q'_1 Q'_2 P'_3 + p_3(1 - \alpha)$
000	$Q'_1 Q'_2 Q'_3$
Total**	$1 + (p_1 + p_2 + p_3)(1 - \alpha)$

\*\* Total = 1 if and only if  $\alpha = 1$ . $\gamma_i$  is the  $i$ th entry of capture history  $\gamma$  $p_i$  is the capture probability of an animal at the  $i$ th sampling occasion $\alpha$  is the probability of correct identification

$$P'_i = p_i \alpha$$

$$Q'_i = (1 - P'_i).$$

The sum of the marginal probabilities exceeds 1 because of the ghost capture histories observed, and these unique characteristics of the data need to be considered when statistical models are developed.

### 2.4.2 Estimation

The typical multinomial approach to building a likelihood for the observed capture histories is invalid because of the dependency between real and ghost histories, and the fact that the total probability here exceeds 1 because of the ghost histories. Thus, we found that building a valid likelihood function was very difficult. The older and simpler methods of unweighted least squares or minimum  $\chi^2$ , both of which have been used for over a hundred years, can be applied to estimate the parameters without the likelihood being specified. This is based on the idea of using the observed values and marginal expected values of  $\mathbf{X}_\gamma$  in a quadratic distance function, and minimizing the quadratic distance function to obtain the estimates. For example, marginal expected values of  $\mathbf{X}_\gamma$  for the 3-sample case can be written as

$$\begin{aligned}
 E[X_{111}] &= N [P'_1 P'_2 P'_3] \\
 E[X_{110}] &= N [P'_1 P'_2 Q'_3] \\
 E[X_{101}] &= N [P'_1 Q'_2 P'_3] \\
 E[X_{100}] &= N [P'_1 Q'_2 Q'_3 + p_1 (1 - \alpha)] \\
 E[X_{011}] &= N [Q'_1 P'_2 P'_3] \\
 E[X_{010}] &= N [Q'_1 P'_2 Q'_3 + p_2 (1 - \alpha)] \\
 E[X_{001}] &= N [Q'_1 Q'_2 P'_3 + p_3 (1 - \alpha)] \\
 E[X_{000}] &= N [Q'_1 Q'_2 Q'_3],
 \end{aligned}$$

where  $X_{000}$  is not observed. Then, the estimates are obtained by minimizing the quadratic distance function

$$\mathcal{F}_{ls} = \sum_{\gamma, \gamma \neq 000} (x_\gamma - E[X_\gamma])^2$$

or

$$\mathcal{F}_{\chi^2} = \sum_{\gamma, \gamma \neq 000} \frac{(x_\gamma - E[X_\gamma])^2}{E[X_\gamma]}$$

where  $x_\gamma$  represents the data and  $X_\gamma$  represents the random variable. These estimates are consistent despite the complex dependencies involved. This is somewhat analogous to using ordinary

least squares when observations are autocorrelated in a time series.

The methods can also be conditioned on the total number of capture histories observed,  $X_{all}$ . The total probability associated with the observed capture histories is

$$p^* = 1 - Q'_1 Q'_2 Q'_3 + (p_1 + p_2 + p_3)(1 - \alpha)$$

for the 3-sample case, or in general,

$$p^* = 1 - \prod_{i=1}^K (1 - P'_i) + \left( \sum_{i=1}^K p_i \right) (1 - \alpha)$$

for the  $K$ -sample case. Then expected values of  $\mathbf{X}_\gamma$  with the conditional approach can be written as

$$E[X_\gamma | X_{all} = x_{all}] = \frac{x_{all} \Pr[\gamma]}{p^*}$$

where  $x_{all}$  is the total number of capture histories observed. Again, the estimates are obtained by minimizing the quadratic distance function  $\mathcal{F}_{ls}$  or  $\mathcal{F}_{\chi^2}$  as described for the unconditional approach. With the conditional approach, the parameter  $N$  is removed from the estimation process and estimated as a derived parameter,

$$\hat{N} = \frac{x_{all}}{\hat{p}^*}.$$

## 2.5 Simulation Study

### 2.5.1 Simulation 1: Cases with Time Specific Capture Probabilities

In our simulation study, we considered a closed population of  $N$  animals, and a capture-recapture study with  $K = 5$  sampling occasions. We allowed for the capture probability to be time dependent, and each animal was subject to capture with probability  $p_i$  at each sampling occasion  $i$ . Whenever an animal was captured, identification of the animal was either correct with probability  $\alpha$ , or incorrect with probability  $(1 - \alpha)$ . When the identification was correct, the real capture history of the animal was recorded as capture (i.e., [1]). However, if the identification was incorrect, the real capture history of the animal was recorded as non-capture (i.e., [0]), and a ghost capture history was created with a capture for the sampling occasion (i.e., [1]). Then, each animal

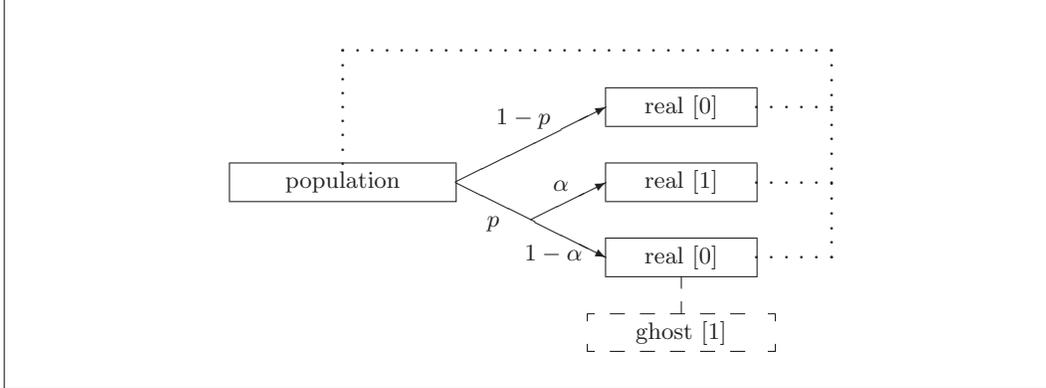


Figure 2.1: A diagram of the misidentification mechanism for non-evolving natural tags 1.

was again subject to capture at the next sampling occasion (see Figure 2.1). Note that a real capture history always has the possibility of recapture. However, a ghost capture history does not have the possibility of recapture, and misidentification always creates a new ghost capture history.

Parameter values were chosen to reflect a wide range of population sizes, capture probabilities and correct identification rates. We considered four specific cases in the simulation study based on different combinations of parameter values.

Case 1:  $N = 1000$  and  $\mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$

Case 2:  $N = 200$  and  $\mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$

Case 3:  $N = 1000$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

Case 4:  $N = 200$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

Each combination of parameter values is describing either a large or a small population size with high or low capture probabilities, and for each case, correct identification rates of  $\alpha = 0.7, 0.8,$  and  $0.9$  were considered.

The estimation methods considered under our NE1 model were unweighted least squares and minimum  $\chi^2$ , based on the quadratic distance functions of  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$ , respectively. In addition, unconditional and conditional (on  $x_{all}$ ) approaches were considered. We were also interested in the comparison of estimates obtained under our NE1 model (**Model NE1<sub>t</sub>**), the model developed by Lukacs and Burnham (2005a) (**Model L&B<sub>t</sub>**) and the corresponding conventional

capture-recapture model (**Model  $M_t$** ). Thus, estimates were also obtained under Model L&B $_t$  by maximizing the conditional likelihood (i.e.,  $f_0$  is not estimated) described in Lukacs and Burnham (2005a, p.398) and under Model  $M_t$  by maximizing the likelihood (conditioned on  $x_{all}$ ) for the same generated data sets.

The performance of the estimators was assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  based on 100 simulated data sets, and if the estimation process failed to converge, those estimates were excluded from the computation of the results. The results for cases 1 to 4 are summarized in Tables 2.4 - 2.7. Although we considered both unconditional and conditional (on  $x_{all}$ ) approaches for the estimator of  $N$  under Model NE1 $_t$ , the unconditional approach displayed numerical problems such as sensitivity to starting values and non-convergence. Thus, only results from the conditional approach are presented in the Tables.

It is clear from the simulation results that  $\hat{N}$  was positively biased when data were analyzed under Model  $M_t$ , in which misidentification is ignored. Such bias in the estimates can be substantial as the correct identification rate becomes lower (relative bias  $> 110\%$  for  $\alpha = 0.7$  cases). The estimates under Model L&B $_t$  were highly variable depending on the starting values we examined, and it was difficult to evaluate the performance of the L&B $_t$  estimator. Thus, we present estimates obtained by using a particular set of starting values in the Tables for comparison purposes. Although the bias in  $\hat{N}$  in the estimates obtained under Model L&B $_t$  (relative bias  $\approx 10 - 85\%$ ) were smaller than that under Model  $M_t$  (relative bias  $\approx 25 - 155\%$ ), these particular results still indicated positive biases in the estimates. Also, in the high capture probability cases, the estimates  $\hat{p}_5$  were usually close to the boundary value 1 under Model L&B $_t$ . The performance of both estimation methods under Model NE1 $_t$  was good, particularly for the cases of high capture probability (relative bias  $< 3\%$  and relative standard error  $< 5\%$  for cases 1 and 2). However, as for the conventional capture-recapture models, the performance was worse when the capture probability was low, and we found an increase in bias in  $\hat{N}$  with the low capture probability cases (relative bias  $\approx 1 - 30\%$  and relative standard error  $\approx 10 - 60\%$  for cases 3 and 4). For case 4 with  $\alpha = 0.7$ , we observed a larger difference between average  $\hat{N}$  from unweighted least squares and minimum  $\chi^2$ . There were more data sets with  $\hat{\alpha} \approx 1$  with unweighted least squares compared to minimum  $\chi^2$ , and results for these data sets tended to inflate the average  $\hat{N}$  from unweighted least squares for this case. Performance of the two estimation methods under Model NE1 $_t$  was similar for the high capture probability cases, but the method of minimum  $\chi^2$  gave smaller root

Table 2.4: [Simulation 1: case 1] Non-evolving natural tags 1 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1000 (21)	1007 (21)	1255 (209)	2531 (54)
$\alpha$	0.7	0.700 (0.008)	0.703 (0.008)	0.590 (0.028)	--
$p_1$	0.7	0.700 (0.026)	0.697 (0.022)	0.334 (0.025)	0.277 (0.009)
$p_2$	0.8	0.797 (0.027)	0.795 (0.022)	0.376 (0.033)	0.316 (0.009)
$p_3$	0.7	0.698 (0.027)	0.695 (0.024)	0.368 (0.047)	0.276 (0.009)
$p_4$	0.8	0.800 (0.026)	0.795 (0.023)	0.560 (0.077)	0.316 (0.009)
$p_5$	0.7	0.699 (0.025)	0.698 (0.019)	0.951 (0.139)	0.277 (0.007)
$c_2$	--	--	--	0.589 (0.056)	--
$c_3$	--	--	--	0.493 (0.043)	--
$c_4$	--	--	--	0.533 (0.033)	--
$c_5$	--	--	--	0.438 (0.029)	--
no. not conv.		0	0	2	0
$\sqrt{\text{MSE}(\hat{N})}$		21.00	22.13	329.70	1531.95
$N$	1000	999 (13)	1004 (12)	1205 (39)	1886 (36)
$\alpha$	0.8	0.799 (0.008)	0.801 (0.008)	0.690 (0.018)	--
$p_1$	0.7	0.700 (0.020)	0.697 (0.017)	0.401 (0.016)	0.371 (0.011)
$p_2$	0.8	0.798 (0.021)	0.798 (0.017)	0.423 (0.020)	0.424 (0.010)
$p_3$	0.7	0.698 (0.021)	0.696 (0.018)	0.381 (0.029)	0.370 (0.011)
$p_4$	0.8	0.801 (0.020)	0.796 (0.016)	0.556 (0.053)	0.424 (0.011)
$p_5$	0.7	0.701 (0.021)	0.700 (0.020)	0.925 (0.111)	0.372 (0.011)
$c_2$	--	--	--	0.654 (0.032)	--
$c_3$	--	--	--	0.555 (0.021)	--
$c_4$	--	--	--	0.614 (0.020)	--
$c_5$	--	--	--	0.505 (0.021)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		13.03	12.64	208.67	886.73
$N$	1000	1000 (8)	1002 (7)	1136 (19)	1400 (22)
$\alpha$	0.9	0.899 (0.005)	0.900 (0.005)	0.824 (0.012)	--
$p_1$	0.7	0.701 (0.018)	0.698 (0.016)	0.508 (0.014)	0.500 (0.013)
$p_2$	0.8	0.803 (0.016)	0.798 (0.015)	0.512 (0.024)	0.572 (0.014)
$p_3$	0.7	0.700 (0.019)	0.699 (0.016)	0.410 (0.030)	0.501 (0.012)
$p_4$	0.8	0.799 (0.015)	0.797 (0.014)	0.550 (0.046)	0.571 (0.013)
$p_5$	0.7	0.701 (0.018)	0.698 (0.017)	0.886 (0.093)	0.500 (0.012)
$c_2$	--	--	--	0.724 (0.017)	--
$c_3$	--	--	--	0.628 (0.016)	--
$c_4$	--	--	--	0.701 (0.014)	--
$c_5$	--	--	--	0.586 (0.016)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		8.00	7.28	137.32	400.60

Table 2.5: [Simulation 1: case 2] Non-evolving natural tags 1 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	198 (10)	205 (9)	244 (17)	509 (23)
$\alpha$	0.7	0.695 (0.018)	0.710 (0.018)	0.582 (0.045)	--
$p_1$	0.7	0.707 (0.059)	0.700 (0.050)	0.336 (0.023)	0.278 (0.019)
$p_2$	0.8	0.806 (0.068)	0.790 (0.049)	0.379 (0.034)	0.316 (0.021)
$p_3$	0.7	0.691 (0.053)	0.688 (0.047)	0.361 (0.039)	0.273 (0.018)
$p_4$	0.8	0.808 (0.059)	0.786 (0.051)	0.565 (0.068)	0.314 (0.016)
$p_5$	0.7	0.703 (0.061)	0.690 (0.046)	0.962 (0.095)	0.275 (0.018)
$c_2$	--	--	--	0.595 (0.075)	--
$c_3$	--	--	--	0.493 (0.060)	--
$c_4$	--	--	--	0.535 (0.054)	--
$c_5$	--	--	--	0.433 (0.050)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		10.19	10.29	47.16	309.85
$N$	200	199 (6)	204 (7)	239 (10)	375 (16)
$\alpha$	0.8	0.799 (0.018)	0.808 (0.017)	0.691 (0.037)	--
$p_1$	0.7	0.702 (0.050)	0.691 (0.037)	0.405 (0.022)	0.373 (0.023)
$p_2$	0.8	0.794 (0.041)	0.782 (0.042)	0.422 (0.027)	0.424 (0.023)
$p_3$	0.7	0.702 (0.051)	0.691 (0.043)	0.385 (0.046)	0.373 (0.023)
$p_4$	0.8	0.805 (0.049)	0.784 (0.042)	0.566 (0.063)	0.427 (0.024)
$p_5$	0.7	0.706 (0.045)	0.696 (0.041)	0.942 (0.080)	0.376 (0.025)
$c_2$	--	--	--	0.649 (0.048)	--
$c_3$	--	--	--	0.558 (0.037)	--
$c_4$	--	--	--	0.619 (0.039)	--
$c_5$	--	--	--	0.508 (0.042)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		6.08	8.06	40.26	175.72
$N$	200	199 (4)	202 (3)	227 (6)	279 (9)
$\alpha$	0.9	0.900 (0.013)	0.903 (0.012)	0.826 (0.030)	--
$p_1$	0.7	0.703 (0.036)	0.693 (0.032)	0.510 (0.028)	0.502 (0.028)
$p_2$	0.8	0.806 (0.038)	0.787 (0.034)	0.510 (0.040)	0.574 (0.029)
$p_3$	0.7	0.705 (0.041)	0.693 (0.031)	0.407 (0.061)	0.503 (0.031)
$p_4$	0.8	0.798 (0.035)	0.785 (0.033)	0.554 (0.079)	0.572 (0.029)
$p_5$	0.7	0.690 (0.038)	0.682 (0.034)	0.871 (0.097)	0.494 (0.029)
$c_2$	--	--	--	0.727 (0.039)	--
$c_3$	--	--	--	0.632 (0.038)	--
$c_4$	--	--	--	0.701 (0.037)	--
$c_5$	--	--	--	0.577 (0.036)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.12	3.60	27.65	79.51

Table 2.6: [Simulation 1: case 3] Non-evolving natural tags 1 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1034 (225)	916 (169)	1212 (193)	2189 (108)
$\alpha$	0.7	0.704 (0.069)	0.680 (0.056)	0.678 (0.079)	--
$p_1$	0.3	0.303 (0.065)	0.340 (0.060)	0.170 (0.019)	0.137 (0.009)
$p_2$	0.2	0.203 (0.048)	0.230 (0.045)	0.116 (0.016)	0.092 (0.008)
$p_3$	0.3	0.303 (0.069)	0.340 (0.062)	0.180 (0.028)	0.137 (0.010)
$p_4$	0.2	0.205 (0.048)	0.232 (0.045)	0.130 (0.023)	0.093 (0.009)
$p_5$	0.3	0.303 (0.067)	0.340 (0.061)	0.205 (0.040)	0.137 (0.010)
$c_2$	--	--	--	0.142 (0.028)	--
$c_3$	--	--	--	0.211 (0.033)	--
$c_4$	--	--	--	0.137 (0.024)	--
$c_5$	--	--	--	0.200 (0.026)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		227.55	188.72	286.69	1193.89
$N$	1000	1048 (209)	946 (165)	1436 (425)	1641 (81)
$\alpha$	0.8	0.813 (0.073)	0.788 (0.062)	0.787 (0.082)	--
$p_1$	0.3	0.297 (0.062)	0.330 (0.061)	0.170 (0.026)	0.183 (0.013)
$p_2$	0.2	0.199 (0.042)	0.223 (0.041)	0.112 (0.020)	0.123 (0.009)
$p_3$	0.3	0.298 (0.061)	0.330 (0.060)	0.166 (0.033)	0.183 (0.013)
$p_4$	0.2	0.196 (0.041)	0.221 (0.040)	0.108 (0.023)	0.121 (0.009)
$p_5$	0.3	0.297 (0.062)	0.329 (0.058)	0.166 (0.041)	0.183 (0.013)
$c_2$	--	--	--	0.162 (0.029)	--
$c_3$	--	--	--	0.240 (0.034)	--
$c_4$	--	--	--	0.156 (0.022)	--
$c_5$	--	--	--	0.230 (0.026)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		214.44	173.61	608.86	646.09
$N$	1000	1014 (132)	956 (108)	1509 (255)	1266 (39)
$\alpha$	0.9	0.904 (0.048)	0.889 (0.041)	0.885 (0.052)	--
$p_1$	0.3	0.302 (0.041)	0.321 (0.037)	0.180 (0.025)	0.238 (0.012)
$p_2$	0.2	0.197 (0.032)	0.214 (0.030)	0.109 (0.018)	0.156 (0.012)
$p_3$	0.3	0.301 (0.043)	0.320 (0.039)	0.158 (0.029)	0.238 (0.012)
$p_4$	0.2	0.199 (0.029)	0.214 (0.026)	0.096 (0.022)	0.157 (0.011)
$p_5$	0.3	0.300 (0.041)	0.319 (0.037)	0.139 (0.035)	0.237 (0.013)
$c_2$	--	--	--	0.180 (0.026)	--
$c_3$	--	--	--	0.275 (0.028)	--
$c_4$	--	--	--	0.179 (0.019)	--
$c_5$	--	--	--	0.265 (0.023)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		132.74	116.61	569.30	268.84

Table 2.7: [Simulation 1: case 4] Non-evolving natural tags 1 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	258 (120)	185 (94)	270 (122)	438 (49)
$\alpha$	0.7	0.761 (0.159)	0.700 (0.132)	0.701 (0.161)	--
$p_1$	0.3	0.297 (0.159)	0.402 (0.154)	0.164 (0.027)	0.139 (0.020)
$p_2$	0.2	0.195 (0.107)	0.277 (0.108)	0.111 (0.027)	0.092 (0.017)
$p_3$	0.3	0.294 (0.159)	0.402 (0.153)	0.173 (0.039)	0.139 (0.019)
$p_4$	0.2	0.196 (0.108)	0.281 (0.116)	0.121 (0.034)	0.093 (0.016)
$p_5$	0.3	0.296 (0.160)	0.402 (0.147)	0.193 (0.060)	0.140 (0.022)
$c_2$	--	--	--	0.144 (0.055)	--
$c_3$	--	--	--	0.211 (0.066)	--
$c_4$	--	--	--	0.141 (0.047)	--
$c_5$	--	--	--	0.204 (0.059)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		133.28	95.18	140.65	242.99
$N$	200	221 (75)	170 (48)	302 (275)	332 (28)
$\alpha$	0.8	0.819 (0.122)	0.770 (0.089)	0.761 (0.132)	--
$p_1$	0.3	0.307 (0.120)	0.386 (0.102)	0.173 (0.041)	0.182 (0.026)
$p_2$	0.2	0.208 (0.085)	0.272 (0.078)	0.116 (0.031)	0.122 (0.019)
$p_3$	0.3	0.304 (0.119)	0.390 (0.105)	0.172 (0.051)	0.182 (0.025)
$p_4$	0.2	0.198 (0.076)	0.266 (0.074)	0.114 (0.038)	0.119 (0.019)
$p_5$	0.3	0.302 (0.118)	0.390 (0.109)	0.175 (0.064)	0.182 (0.020)
$c_2$	--	--	--	0.165 (0.058)	--
$c_3$	--	--	--	0.249 (0.063)	--
$c_4$	--	--	--	0.158 (0.042)	--
$c_5$	--	--	--	0.246 (0.057)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		77.88	56.60	293.30	134.93
$N$	200	209 (44)	181 (37)	367 (239)	258 (22)
$\alpha$	0.9	0.906 (0.087)	0.877 (0.081)	0.870 (0.101)	--
$p_1$	0.3	0.302 (0.072)	0.356 (0.075)	0.165 (0.046)	0.236 (0.036)
$p_2$	0.2	0.202 (0.062)	0.250 (0.066)	0.101 (0.032)	0.157 (0.024)
$p_3$	0.3	0.302 (0.077)	0.358 (0.082)	0.148 (0.058)	0.236 (0.036)
$p_4$	0.2	0.202 (0.058)	0.248 (0.064)	0.089 (0.050)	0.156 (0.026)
$p_5$	0.3	0.295 (0.082)	0.352 (0.084)	0.126 (0.075)	0.231 (0.035)
$c_2$	--	--	--	0.192 (0.068)	--
$c_3$	--	--	--	0.272 (0.060)	--
$c_4$	--	--	--	0.181 (0.046)	--
$c_5$	--	--	--	0.268 (0.050)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		44.91	41.59	291.56	62.03

mean square errors in the cases with low capture probabilities.

An important result here is that ignoring misidentification can lead to overestimation of  $N$  as indicated by other studies (e.g., Creel et al., 2003). The larger the rate of misidentification, the larger the positive bias in  $\hat{N}$ , and the magnitude of such bias in the estimates can be substantial as shown by the results. There were cases in which the performance of the  $NE1_t$  estimator was not good. However, even for those cases, bias in estimates of  $N$  tended to be much smaller than those under Model  $M_t$  and Model L&B $_t$ .

### 2.5.2 Simulation 2: Cases with Time Specific Capture Probabilities (High $\alpha$ )

Although error rates in DNA fingerprints can vary widely (Waits, 2004), they can be reduced greatly through careful considerations on field methods, laboratory techniques, and so on (Paetkau, 2003). Thus, the misidentification rates in reality can be lower than the values we examined in Simulation 1. Lukacs and Burnham (2005a) considered only very high correct identification rates, which are probably reasonable for some genetic tag-based capture-recapture studies. Thus, in this simulation, we considered lower misidentification rates, and generated new sets of data with correct identification rates of  $\alpha = 0.950, 0.975$  and  $1.000$  for the four cases described in the previous section.

With the lower misidentification rates, we were interested in examining (1) whether the  $NE1_t$  estimator can effectively estimate  $\alpha$ , (2) whether estimates under Model L&B $_t$  improve, and (3) how well the  $M_t$  estimator can perform, or in other words, whether estimates under Model  $M_t$  can be reasonable approximations. Thus, each generated data set was analyzed by using the two estimation methods under Model  $NE1_t$ , and also maximum likelihood estimates under Model L&B $_t$  and Model  $M_t$  were obtained for the same generated data sets. The results for cases 1 to 4 are summarized in Tables 2.8 - 2.11. Again, the unconditional approach under Model  $NE1_t$  displayed numerical problems, and we have only included the results from the conditional (on  $x_{all}$ ) approach in the Tables.

As we expected, performance of the  $M_t$  estimator improved as the value of  $\alpha$  increased. However, there was still substantial positive bias in  $\hat{N}$ , even for the cases of  $\alpha = 0.975$  (relative bias  $\approx 10 - 20\%$  and  $5 - 10\%$  for  $\alpha = 0.950$  and  $0.975$ , respectively). The performance of both

Table 2.8: [Simulation 2: case 1] Non-evolving natural tags 1 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>t</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1000 (6)	1001 (5)	1090 (14)	1192 (16)
$\alpha$	0.950	0.950 (0.004)	0.950 (0.004)	0.911 (0.010)	--
$p_1$	0.7	0.698 (0.021)	0.697 (0.015)	0.584 (0.016)	0.587 (0.015)
$p_2$	0.8	0.801 (0.016)	0.797 (0.014)	0.594 (0.027)	0.671 (0.014)
$p_3$	0.7	0.697 (0.021)	0.696 (0.015)	0.436 (0.038)	0.585 (0.015)
$p_4$	0.8	0.799 (0.014)	0.797 (0.012)	0.530 (0.059)	0.671 (0.014)
$p_5$	0.7	0.702 (0.020)	0.699 (0.017)	0.746 (0.107)	0.588 (0.016)
$c_2$	--	--	--	0.762 (0.016)	--
$c_3$	--	--	--	0.661 (0.016)	--
$c_4$	--	--	--	0.747 (0.014)	--
$c_5$	--	--	--	0.635 (0.017)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		6.00	5.09	91.08	192.66
$N$	1000	999 (6)	999 (5)	1058 (12)	1094 (10)
$\alpha$	0.975	0.975 (0.003)	0.975 (0.003)	0.957 (0.008)	--
$p_1$	0.7	0.701 (0.017)	0.698 (0.015)	0.633 (0.016)	0.640 (0.015)
$p_2$	0.8	0.802 (0.017)	0.799 (0.015)	0.662 (0.032)	0.732 (0.015)
$p_3$	0.7	0.702 (0.019)	0.700 (0.016)	0.470 (0.047)	0.641 (0.015)
$p_4$	0.8	0.799 (0.015)	0.797 (0.014)	0.508 (0.069)	0.730 (0.014)
$p_5$	0.7	0.701 (0.019)	0.698 (0.016)	0.607 (0.134)	0.640 (0.015)
$c_2$	--	--	--	0.782 (0.017)	--
$c_3$	--	--	--	0.682 (0.016)	--
$c_4$	--	--	--	0.770 (0.014)	--
$c_5$	--	--	--	0.663 (0.016)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		6.08	5.09	59.22	94.53
$N$	1000	997 (3)	997 (3)	1043 (81)	1000 (1)
$\alpha$	1.000	0.999 (0.001)	0.999 (0.001)	0.999 (0.002)	--
$p_1$	0.7	0.701 (0.018)	0.701 (0.015)	0.674 (0.040)	0.702 (0.015)
$p_2$	0.8	0.800 (0.015)	0.797 (0.014)	0.716 (0.094)	0.799 (0.013)
$p_3$	0.7	0.701 (0.015)	0.698 (0.013)	0.480 (0.159)	0.699 (0.013)
$p_4$	0.8	0.802 (0.015)	0.798 (0.013)	0.354 (0.208)	0.800 (0.013)
$p_5$	0.7	0.698 (0.018)	0.697 (0.014)	0.122 (0.136)	0.698 (0.013)
$c_2$	--	--	--	0.799 (0.015)	--
$c_3$	--	--	--	0.700 (0.013)	--
$c_4$	--	--	--	0.801 (0.014)	--
$c_5$	--	--	--	0.699 (0.013)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.24	4.24	91.70	1.00

Table 2.9: [Simulation 2: case 2] Non-evolving natural tags 1 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>t</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	199 (3)	200 (3)	217 (4)	237 (6)
$\alpha$	0.950	0.951 (0.009)	0.951 (0.009)	0.913 (0.023)	--
$p_1$	0.7	0.700 (0.038)	0.692 (0.032)	0.587 (0.029)	0.589 (0.030)
$p_2$	0.8	0.796 (0.031)	0.784 (0.029)	0.594 (0.048)	0.670 (0.026)
$p_3$	0.7	0.704 (0.043)	0.692 (0.039)	0.441 (0.077)	0.588 (0.034)
$p_4$	0.8	0.799 (0.036)	0.788 (0.034)	0.541 (0.107)	0.674 (0.031)
$p_5$	0.7	0.708 (0.041)	0.698 (0.034)	0.741 (0.126)	0.593 (0.032)
$c_2$	--	--	--	0.760 (0.036)	--
$c_3$	--	--	--	0.662 (0.038)	--
$c_4$	--	--	--	0.747 (0.036)	--
$c_5$	--	--	--	0.640 (0.036)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	3.00	17.46	37.48
$N$	200	199 (3)	199 (2)	211 (4)	218 (4)
$\alpha$	0.975	0.975 (0.008)	0.975 (0.007)	0.957 (0.018)	--
$p_1$	0.7	0.705 (0.037)	0.695 (0.031)	0.635 (0.031)	0.641 (0.031)
$p_2$	0.8	0.803 (0.035)	0.788 (0.030)	0.661 (0.065)	0.733 (0.032)
$p_3$	0.7	0.704 (0.040)	0.695 (0.030)	0.475 (0.101)	0.643 (0.032)
$p_4$	0.8	0.800 (0.035)	0.788 (0.027)	0.522 (0.149)	0.731 (0.030)
$p_5$	0.7	0.692 (0.039)	0.685 (0.033)	0.571 (0.171)	0.632 (0.033)
$c_2$	--	--	--	0.784 (0.033)	--
$c_3$	--	--	--	0.685 (0.034)	--
$c_4$	--	--	--	0.770 (0.031)	--
$c_5$	--	--	--	0.655 (0.035)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	2.23	11.70	18.43
$N$	200	198 (1)	198 (1)	209 (25)	199 (1)
$\alpha$	1.000	0.998 (0.002)	0.998 (0.003)	0.998 (0.003)	--
$p_1$	0.7	0.699 (0.040)	0.688 (0.032)	0.667 (0.057)	0.693 (0.033)
$p_2$	0.8	0.808 (0.034)	0.794 (0.028)	0.728 (0.132)	0.804 (0.028)
$p_3$	0.7	0.711 (0.035)	0.702 (0.027)	0.560 (0.237)	0.708 (0.029)
$p_4$	0.8	0.804 (0.030)	0.790 (0.027)	0.551 (0.368)	0.800 (0.028)
$p_5$	0.7	0.709 (0.043)	0.701 (0.035)	0.155 (0.275)	0.706 (0.037)
$c_2$	--	--	--	0.807 (0.030)	--
$c_3$	--	--	--	0.710 (0.029)	--
$c_4$	--	--	--	0.801 (0.028)	--
$c_5$	--	--	--	0.707 (0.037)	--
no. not conv.		0	0	4	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	2.23	26.57	1.41

Table 2.10: [Simulation 2: case 3] Non-evolving natural tags 1 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>t</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1014 (113)	969 (110)	1763 (835)	1128 (39)
$\alpha$	0.950	0.953 (0.047)	0.940 (0.046)	0.930 (0.054)	--
$p_1$	0.3	0.300 (0.041)	0.316 (0.042)	0.174 (0.041)	0.266 (0.016)
$p_2$	0.2	0.202 (0.028)	0.214 (0.029)	0.104 (0.029)	0.178 (0.013)
$p_3$	0.3	0.300 (0.037)	0.316 (0.040)	0.145 (0.042)	0.266 (0.017)
$p_4$	0.2	0.197 (0.026)	0.212 (0.027)	0.083 (0.029)	0.176 (0.012)
$p_5$	0.3	0.299 (0.040)	0.316 (0.040)	0.115 (0.048)	0.266 (0.015)
$c_2$	--	--	--	0.193 (0.029)	--
$c_3$	--	--	--	0.287 (0.030)	--
$c_4$	--	--	--	0.191 (0.020)	--
$c_5$	--	--	--	0.285 (0.021)	--
no. not conv.		0	0	3	0
$\sqrt{\text{MSE}(\hat{N})}$		113.86	114.28	1131.10	133.80
$N$	1000	982 (80)	948 (72)	1937 (2117)	1058 (27)
$\alpha$	0.975	0.968 (0.033)	0.958 (0.032)	0.953 (0.038)	--
$p_1$	0.3	0.308 (0.031)	0.321 (0.027)	0.179 (0.051)	0.284 (0.014)
$p_2$	0.2	0.202 (0.024)	0.214 (0.023)	0.104 (0.037)	0.187 (0.014)
$p_3$	0.3	0.308 (0.031)	0.321 (0.029)	0.145 (0.057)	0.284 (0.014)
$p_4$	0.2	0.204 (0.023)	0.214 (0.021)	0.083 (0.043)	0.188 (0.013)
$p_5$	0.3	0.308 (0.029)	0.320 (0.028)	0.117 (0.074)	0.283 (0.015)
$c_2$	--	--	--	0.195 (0.024)	--
$c_3$	--	--	--	0.302 (0.025)	--
$c_4$	--	--	--	0.198 (0.018)	--
$c_5$	--	--	--	0.296 (0.020)	--
no. not conv.		0	0	2	0
$\sqrt{\text{MSE}(\hat{N})}$		82.00	88.81	2315.09	63.97
$N$	1000	962 (48)	946 (55)	1990 (1713)	1003 (25)
$\alpha$	1.000	0.983 (0.022)	0.979 (0.024)	0.971 (0.030)	--
$p_1$	0.3	0.313 (0.024)	0.319 (0.025)	0.177 (0.054)	0.298 (0.015)
$p_2$	0.2	0.210 (0.019)	0.217 (0.019)	0.104 (0.038)	0.201 (0.015)
$p_3$	0.3	0.317 (0.025)	0.323 (0.025)	0.143 (0.067)	0.301 (0.015)
$p_4$	0.2	0.210 (0.019)	0.218 (0.018)	0.082 (0.058)	0.201 (0.014)
$p_5$	0.3	0.310 (0.024)	0.317 (0.026)	0.109 (0.096)	0.297 (0.017)
$c_2$	--	--	--	0.206 (0.027)	--
$c_3$	--	--	--	0.310 (0.024)	--
$c_4$	--	--	--	0.207 (0.017)	--
$c_5$	--	--	--	0.306 (0.022)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		61.22	77.07	1978.50	25.17

Table 2.11: [Simulation 2: case 4] Non-evolving natural tags 1 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	202 (31)	181 (30)	356 (226)	228 (16)
$\alpha$	0.950	0.947 (0.062)	0.922 (0.062)	0.909 (0.079)	--
$p_1$	0.3	0.309 (0.068)	0.348 (0.065)	0.173 (0.047)	0.264 (0.035)
$p_2$	0.2	0.206 (0.052)	0.245 (0.056)	0.106 (0.036)	0.178 (0.026)
$p_3$	0.3	0.306 (0.067)	0.349 (0.068)	0.146 (0.052)	0.265 (0.035)
$p_4$	0.2	0.201 (0.049)	0.240 (0.053)	0.086 (0.040)	0.173 (0.027)
$p_5$	0.3	0.300 (0.060)	0.350 (0.069)	0.116 (0.065)	0.265 (0.030)
$c_2$	--	--	--	0.194 (0.054)	--
$c_3$	--	--	--	0.293 (0.063)	--
$c_4$	--	--	--	0.188 (0.040)	--
$c_5$	--	--	--	0.295 (0.042)	--
no. not conv.		0	0	2	0
$\sqrt{\text{MSE}(\hat{N})}$		31.06	35.51	274.61	32.24
$N$	200	195 (27)	180 (26)	372 (204)	215 (14)
$\alpha$	0.975	0.958 (0.059)	0.943 (0.057)	0.931 (0.068)	--
$p_1$	0.3	0.317 (0.058)	0.350 (0.060)	0.172 (0.052)	0.282 (0.039)
$p_2$	0.2	0.212 (0.056)	0.246 (0.054)	0.101 (0.034)	0.188 (0.026)
$p_3$	0.3	0.317 (0.064)	0.352 (0.069)	0.140 (0.053)	0.283 (0.040)
$p_4$	0.2	0.211 (0.049)	0.243 (0.054)	0.076 (0.031)	0.187 (0.030)
$p_5$	0.3	0.309 (0.067)	0.345 (0.066)	0.103 (0.051)	0.277 (0.039)
$c_2$	--	--	--	0.207 (0.066)	--
$c_3$	--	--	--	0.299 (0.057)	--
$c_4$	--	--	--	0.202 (0.046)	--
$c_5$	--	--	--	0.300 (0.047)	--
no. not conv.		0	0	3	0
$\sqrt{\text{MSE}(\hat{N})}$		27.45	32.80	266.83	20.51
$N$	200	186 (24)	174 (21)	465 (329)	199 (11)
$\alpha$	1.000	0.969 (0.055)	0.956 (0.051)	0.951 (0.063)	--
$p_1$	0.3	0.330 (0.064)	0.358 (0.059)	0.157 (0.059)	0.303 (0.038)
$p_2$	0.2	0.221 (0.053)	0.253 (0.045)	0.090 (0.041)	0.203 (0.030)
$p_3$	0.3	0.335 (0.066)	0.363 (0.061)	0.123 (0.068)	0.306 (0.036)
$p_4$	0.2	0.219 (0.052)	0.251 (0.054)	0.064 (0.037)	0.201 (0.031)
$p_5$	0.3	0.334 (0.066)	0.360 (0.057)	0.089 (0.061)	0.303 (0.036)
$c_2$	--	--	--	0.215 (0.054)	--
$c_3$	--	--	--	0.322 (0.053)	--
$c_4$	--	--	--	0.214 (0.044)	--
$c_5$	--	--	--	0.316 (0.044)	--
no. not conv.		0	0	2	0
$\sqrt{\text{MSE}(\hat{N})}$		27.78	33.42	422.45	11.04

estimation methods under Model  $NE1_t$  was good for the high capture probability cases (relative bias  $\leq 1\%$  and relative standard error  $< 2\%$  for cases 1 and 2). The low capture probability cases indicated bias in  $\hat{N}$  in general, particularly for case 4 with the minimum  $\chi^2$  method (relative bias  $\approx 9 - 13\%$  and relative standard error  $\approx 10 - 15\%$ ). As in Simulation 1, the estimates under Model  $L\&B_t$  varied depending on the starting values, and here we present the estimates obtained by using a particular set of starting values in the Tables for comparison purposes. For high capture probability cases, these particular results under Model  $L\&B_t$  improved as the value of  $\alpha$  increased (relative bias  $< 10\%$  and relative standard error  $< 13\%$  for cases 1 and 2). However, the performance of  $L\&B_t$  estimator was poor for the cases with low capture probability (relative bias  $> 75\%$  and relative standard error  $> 80\%$  for cases 3 and 4).

The important message here is that the effect of misidentification on the estimates under the  $M_t$  estimator was more serious than we expected, and ignoring misidentification can lead to substantial positive bias in  $\hat{N}$ . On the other hand, the performance of the  $NE1_t$  estimator was good, especially for high capture probability cases. However, some bias was noted for the low capture probability cases, and such bias in the estimates increases as the value of  $\alpha$  approaches 1. Sensitivity to starting values seemed to be a persisting problem of the  $L\&B_t$  estimator throughout Simulations 1 and 2, and we believe this is caused by non-identifiability of the model when  $p$  and  $c$  are time specific. The results here indicate that performance of the  $L\&B_t$  estimator was clearly inferior to the performance of the  $NE1_t$  estimators for data generated under the misidentification mechanism  $NE1$ .

### 2.5.3 Simulation 3: Cases with Constant Capture Probability

In this simulation, we assumed a constant capture probability,  $p$ . Here, we again considered a closed population of  $N$  animals, and a capture-recapture study with  $K = 5$  sampling occasions. The parameter values were chosen to follow the four cases in Simulation 1, and new sets of data were generated by assuming a constant capture probability.

Case 1:  $N = 1000$  and  $p = 0.8$

Case 2:  $N = 200$  and  $p = 0.8$

Case 3:  $N = 1000$  and  $p = 0.3$

Case 4:  $N = 200$  and  $p = 0.3$

Each combination of parameter values is describing either a large or a small population size with high or low capture probability, and for each case, correct identification rates of  $\alpha = 0.7, 0.8, 0.9, 0.950, 0.975$  and  $1.000$  were considered.

The data sets were analyzed by using two different estimation methods, unweighted least squares and minimum  $\chi^2$ , under a version of Model NE1 that assumes constant capture probabilities (**Model NE1<sub>0</sub>**). Only the conditional approach (on  $x_{all}$ ) was considered here. Also, we were interested in the loss of precision when the data generated assuming constant capture probability are analyzed under models that assume time specific capture probabilities. Thus, the same data sets were also analyzed by using two different estimation methods under **Model NE1<sub>t</sub>**. In addition, we were interested in the comparison of estimates obtained under NE1 models, L&B models and conventional capture-recapture models. Thus, the conditional likelihood estimates under Model L&B (**Model L&B<sub>0</sub>** and **Model L&B<sub>t</sub>**) and the maximum likelihood estimates under conventional capture-recapture models (**Model M<sub>0</sub>** and **Model M<sub>t</sub>**) were also obtained for the same generated data sets.

The performance of estimators under the four models was assessed by examining the average estimates, standard errors and root mean square errors on  $\hat{N}$  over 100 simulated data sets. The results for cases 1 to 4 are summarized in Tables 2.12 - 2.19. Results in Tables 2.12 - 2.15 are from models that assume constant capture probability whereas those in Tables 2.16 - 2.19 are from models that assume time specific capture probabilities.

The results under models that assume constant capture probability indicated the same tendency as in Simulations 1 and 2.  $\hat{N}$  was positively biased when data were analyzed under conventional capture-recapture model (Model M<sub>0</sub>), and such bias in the estimates can be substantial as the correct identification rate becomes lower (relative bias  $> 120\%$  for  $\alpha = 0.7$  cases). The performance of both estimation methods under Model NE1<sub>0</sub> was good, particularly for the cases of high capture probability (relative bias  $< 4\%$  and relative standard error  $< 4\%$  for cases 1 and 2). However, as for the cases in Simulations 1 and 2, an increase in bias in  $\hat{N}$  was evident for low capture probability cases (relative bias  $\approx 1 - 20\%$  and relative standard error  $\approx 4 - 52\%$  for cases 3 and 4). The differences in precision of  $\hat{N}$  under Model NE1<sub>0</sub> and Model NE1<sub>t</sub> were small (the difference was less than 5% when relative standard errors were compared case by case). The estimates from Model L&B<sub>0</sub> did not vary depending on the starting values, and the performance of the estimator was better compared to the cases with time specific capture probabilities examined

Table 2.12: [Simulation 3: case 1] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>0</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>0</sub>		Model L&B <sub>0</sub>	Model M <sub>0</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	998 (14)	1007 (14)	1571 (42)	2599 (60)
$\alpha$	0.7	0.699 (0.008)	0.702 (0.008)	0.559 (0.011)	--
$p$	0.8	0.801 (0.012)	0.797 (0.011)	0.260 (0.010)	0.308 (0.007)
$c$	--	--	--	0.536 (0.010)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		14.14	15.65	572.54	1600.12
$N$	1000	1000 (12)	1006 (11)	1342 (26)	1933 (33)
$\alpha$	0.8	0.799 (0.006)	0.801 (0.006)	0.661 (0.011)	--
$p$	0.8	0.801 (0.013)	0.797 (0.012)	0.354 (0.010)	0.414 (0.008)
$c$	--	--	--	0.618 (0.011)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		12.00	12.52	342.98	933.58
$N$	1000	999 (7)	1003 (5)	1161 (14)	1421 (20)
$\alpha$	0.9	0.900 (0.005)	0.901 (0.005)	0.804 (0.011)	--
$p$	0.8	0.800 (0.010)	0.796 (0.008)	0.498 (0.012)	0.563 (0.008)
$c$	--	--	--	0.703 (0.008)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	5.83	161.60	421.47
$N$	1000	1000 (5)	1001 (4)	1086 (10)	1207 (14)
$\alpha$	0.950	0.949 (0.004)	0.949 (0.004)	0.895 (0.009)	--
$p$	0.8	0.800 (0.009)	0.798 (0.007)	0.609 (0.013)	0.663 (0.009)
$c$	--	--	--	0.749 (0.008)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		5.00	4.12	86.57	1600.12
$N$	1000	1000 (4)	1000 (3)	1047 (7)	1100 (9)
$\alpha$	0.975	0.975 (0.003)	0.975 (0.002)	0.951 (0.007)	--
$p$	0.8	0.800 (0.009)	0.797 (0.007)	0.690 (0.014)	0.726 (0.008)
$c$	--	--	--	0.772 (0.008)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	3.00	47.51	933.58
$N$	1000	998 (2)	998 (2)	999 (1)	1000 (1)
$\alpha$	1.000	1.000 (0.001)	1.000 (0.001)	1.000 (0.001)	--
$p$	0.8	0.801 (0.008)	0.798 (0.006)	0.801 (0.010)	0.800 (0.005)
$c$	--	--	--	0.800 (0.006)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.82	2.82	1.41	421.47

Table 2.13: [Simulation 3: case 2] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>0</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>0</sub>		Model L&B <sub>0</sub>	Model M <sub>0</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	199 (7)	207 (6)	312 (17)	520 (24)
$\alpha$	0.7	0.699 (0.017)	0.712 (0.017)	0.558 (0.024)	--
$p$	0.8	0.802 (0.033)	0.781 (0.030)	0.263 (0.019)	0.308 (0.015)
$c$	--	--	--	0.534 (0.025)	--
no. not conv.		0	0	4	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	9.21	113.28	320.89
$N$	200	200 (4)	206 (4)	269 (12)	385 (17)
$\alpha$	0.8	0.800 (0.016)	0.809 (0.015)	0.665 (0.026)	--
$p$	0.8	0.798 (0.026)	0.780 (0.021)	0.355 (0.025)	0.415 (0.019)
$c$	--	--	--	0.616 (0.022)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	7.21	70.03	185.77
$N$	200	199 (3)	202 (3)	232 (6)	286 (9)
$\alpha$	0.9	0.897 (0.011)	0.900 (0.011)	0.798 (0.025)	--
$p$	0.8	0.801 (0.019)	0.786 (0.016)	0.497 (0.027)	0.559 (0.021)
$c$	--	--	--	0.702 (0.019)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	3.60	32.55	86.46
$N$	200	199 (2)	200 (2)	217 (4)	241 (6)
$\alpha$	0.950	0.949 (0.008)	0.950 (0.008)	0.899 (0.021)	--
$p$	0.8	0.799 (0.021)	0.787 (0.015)	0.608 (0.029)	0.633 (0.020)
$c$	--	--	--	0.747 (0.018)	--
no. not conv.		0	0	4	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	2.00	17.46	320.89
$N$	200	199 (2)	199 (2)	209 (3)	220 (4)
$\alpha$	0.975	0.974 (0.006)	0.974 (0.006)	0.948 (0.016)	--
$p$	0.8	0.800 (0.017)	0.788 (0.013)	0.693 (0.032)	0.726 (0.018)
$c$	--	--	--	0.772 (0.015)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	2.23	9.48	185.77
$N$	200	199 (1)	199 (1)	199 (5)	200 (1)
$\alpha$	1.000	0.999 (0.001)	0.999 (0.001)	0.999 (0.002)	--
$p$	0.8	0.803 (0.016)	0.789 (0.014)	0.804 (0.027)	0.801 (0.013)
$c$	--	--	--	0.802 (0.016)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		1.41	1.41	5.09	86.46

Table 2.14: [Simulation 3: case 3] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>0</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>0</sub>		Model L&B <sub>0</sub>	Model M <sub>0</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1039 (171)	964 (141)	1538 (228)	2217 (99)
$\alpha$	0.7	0.707 (0.051)	0.695 (0.045)	0.678 (0.064)	--
$p$	0.3	0.297 (0.052)	0.322 (0.050)	0.129 (0.017)	0.136 (0.006)
$c$	--	--	--	0.202 (0.021)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		175.39	145.52	584.31	1221.02
$N$	1000	1031 (148)	967 (107)	1327 (120)	1654 (61)
$\alpha$	0.8	0.809 (0.047)	0.796 (0.037)	0.780 (0.055)	--
$p$	0.3	0.296 (0.041)	0.317 (0.033)	0.175 (0.016)	0.182 (0.007)
$c$	--	--	--	0.234 (0.018)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		151.21	111.97	348.32	656.83
$N$	1000	1015 (112)	981 (93)	1145 (83)	1277 (32)
$\alpha$	0.9	0.905 (0.041)	0.897 (0.036)	0.886 (0.052)	--
$p$	0.3	0.299 (0.033)	0.312 (0.030)	0.231 (0.018)	0.236 (0.008)
$c$	--	--	--	0.268 (0.018)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		113.00	94.92	167.07	278.84
$N$	1000	1012 (83)	998 (76)	1073 (58)	1130 (29)
$\alpha$	0.950	0.954 (0.032)	0.948 (0.030)	0.941 (0.041)	--
$p$	0.3	0.298 (0.026)	0.308 (0.024)	0.262 (0.017)	0.266 (0.009)
$c$	--	--	--	0.284 (0.015)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		83.86	76.02	93.23	1130.37
$N$	1000	995 (71)	979 (69)	1028 (49)	1065 (22)
$\alpha$	0.975	0.972 (0.027)	0.968 (0.027)	0.963 (0.036)	--
$p$	0.3	0.304 (0.024)	0.311 (0.023)	0.282 (0.018)	0.282 (0.009)
$c$	--	--	--	0.294 (0.016)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		71.17	72.12	56.43	68.62
$N$	1000	970 (41)	961 (43)	981 (40)	998 (16)
$\alpha$	1.000	0.989 (0.017)	0.987 (0.018)	0.984 (0.025)	--
$p$	0.3	0.311 (0.015)	0.315 (0.017)	0.302 (0.019)	0.301 (0.009)
$c$	--	--	--	0.306 (0.012)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		50.80	58.05	44.28	16.12

Table 2.15: [Simulation 3: case 4] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>0</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>0</sub>		Model L&B <sub>0</sub>	Model M <sub>0</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	238 (103)	188 (56)	344 (107)	446 (55)
$\alpha$	0.7	0.740 (0.127)	0.708 (0.088)	0.715 (0.140)	--
$p$	0.3	0.296 (0.108)	0.360 (0.095)	0.131 (0.035)	0.137 (0.016)
$c$	--	--	--	0.199 (0.044)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		109.78	57.27	179.40	252.07
$N$	200	207 (54)	185 (38)	282 (75)	333 (31)
$\alpha$	0.8	0.808 (0.089)	0.797 (0.067)	0.789 (0.103)	--
$p$	0.3	0.308 (0.079)	0.349 (0.068)	0.174 (0.041)	0.181 (0.018)
$c$	--	--	--	0.234 (0.039)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		54.45	40.85	111.12	136.56
$N$	200	204 (34)	189 (28)	233 (36)	257 (16)
$\alpha$	0.9	0.905 (0.067)	0.893 (0.058)	0.884 (0.087)	--
$p$	0.3	0.304 (0.059)	0.336 (0.053)	0.232 (0.040)	0.235 (0.020)
$c$	--	--	--	0.270 (0.036)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		34.23	30.08	48.83	59.20
$N$	200	199 (27)	189 (24)	217 (27)	225 (13)
$\alpha$	0.950	0.949 (0.053)	0.941 (0.045)	0.941 (0.065)	--
$p$	0.3	0.308 (0.049)	0.332 (0.047)	0.261 (0.040)	0.266 (0.020)
$c$	--	--	--	0.286 (0.032)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		27.01	26.40	31.90	28.17
$N$	200	192 (21)	185 (20)	202 (21)	212 (9)
$\alpha$	0.975	0.962 (0.045)	0.956 (0.042)	0.945 (0.063)	--
$p$	0.3	0.319 (0.042)	0.339 (0.041)	0.285 (0.041)	0.285 (0.020)
$c$	--	--	--	0.303 (0.029)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		22.47	25.00	21.09	15.00
$N$	200	185 (18)	181 (17)	196 (17)	201 (8)
$\alpha$	1.000	0.969 (0.040)	0.966 (0.037)	0.964 (0.051)	--
$p$	0.3	0.331 (0.038)	0.346 (0.037)	0.300 (0.041)	0.300 (0.018)
$c$	--	--	--	0.313 (0.028)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		23.43	25.49	17.46	8.06

Table 2.16: [Simulation 3: case 1] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	998 (14)	1005 (14)	1230 (91)	2599 (60)
$\alpha$	0.7	0.699 (0.008)	0.701 (0.008)	0.563 (0.043)	--
$p_1$	0.8	0.800 (0.021)	0.796 (0.018)	0.369 (0.018)	0.307 (0.008)
$p_2$	0.8	0.799 (0.023)	0.799 (0.017)	0.354 (0.032)	0.308 (0.008)
$p_3$	0.8	0.800 (0.025)	0.798 (0.018)	0.391 (0.032)	0.308 (0.010)
$p_4$	0.8	0.803 (0.024)	0.796 (0.017)	0.527 (0.046)	0.308 (0.009)
$p_5$	0.8	0.804 (0.028)	0.798 (0.016)	0.996 (0.008)	0.308 (0.009)
$c_2$	--	--	--	0.606 (0.082)	--
$c_3$	--	--	--	0.569 (0.043)	--
$c_4$	--	--	--	0.539 (0.039)	--
$c_5$	--	--	--	0.507 (0.049)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		14.14	14.86	247.34	1600.12
$N$	1000	999 (12)	1005 (11)	1230 (204)	1933 (33)
$\alpha$	0.8	0.799 (0.006)	0.800 (0.006)	0.667 (0.023)	--
$p_1$	0.8	0.801 (0.018)	0.799 (0.018)	0.440 (0.032)	0.415 (0.009)
$p_2$	0.8	0.803 (0.019)	0.797 (0.017)	0.384 (0.036)	0.415 (0.009)
$p_3$	0.8	0.798 (0.023)	0.798 (0.018)	0.393 (0.047)	0.414 (0.010)
$p_4$	0.8	0.800 (0.017)	0.797 (0.018)	0.513 (0.075)	0.414 (0.009)
$p_5$	0.8	0.802 (0.019)	0.797 (0.019)	0.932 (0.137)	0.415 (0.010)
$c_2$	--	--	--	0.653 (0.040)	--
$c_3$	--	--	--	0.643 (0.027)	--
$c_4$	--	--	--	0.620 (0.032)	--
$c_5$	--	--	--	0.578 (0.029)	--
no. not conv.		0	0	2	0
$\sqrt{\text{MSE}(\hat{N})}$		12.04	12.08	307.43	933.58
$N$	1000	999 (7)	1002 (5)	1134 (11)	1421 (20)
$\alpha$	0.9	0.900 (0.005)	0.900 (0.005)	0.808 (0.011)	--
$p_1$	0.8	0.801 (0.016)	0.797 (0.015)	0.570 (0.010)	0.563 (0.011)
$p_2$	0.8	0.800 (0.018)	0.798 (0.016)	0.469 (0.020)	0.563 (0.012)
$p_3$	0.8	0.801 (0.018)	0.797 (0.014)	0.418 (0.028)	0.562 (0.013)
$p_4$	0.8	0.799 (0.016)	0.795 (0.013)	0.519 (0.036)	0.562 (0.010)
$p_5$	0.8	0.802 (0.017)	0.796 (0.015)	0.946 (0.042)	0.563 (0.012)
$c_2$	--	--	--	0.720 (0.018)	--
$c_3$	--	--	--	0.719 (0.016)	--
$c_4$	--	--	--	0.702 (0.013)	--
$c_5$	--	--	--	0.673 (0.016)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	5.38	134.45	421.47

Table 2.16 (continued.)

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1000 (5)	1000 (4)	1085 (12)	1207 (14)
$\alpha$	0.950	0.949 (0.004)	0.949 (0.004)	0.897 (0.010)	--
$p_1$	0.8	0.801 (0.016)	0.799 (0.013)	0.663 (0.013)	0.664 (0.012)
$p_2$	0.8	0.800 (0.016)	0.797 (0.012)	0.548 (0.026)	0.664 (0.013)
$p_3$	0.8	0.801 (0.019)	0.798 (0.015)	0.454 (0.042)	0.662 (0.014)
$p_4$	0.8	0.800 (0.017)	0.798 (0.014)	0.506 (0.067)	0.663 (0.012)
$p_5$	0.8	0.800 (0.018)	0.798 (0.015)	0.875 (0.092)	0.664 (0.013)
$c_2$	--	--	--	0.760 (0.015)	--
$c_3$	--	--	--	0.759 (0.015)	--
$c_4$	--	--	--	0.750 (0.014)	--
$c_5$	--	--	--	0.729 (0.017)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		5.00	4.00	85.84	207.47
$N$	1000	1000 (5)	999 (3)	1053 (9)	1100 (9)
$\alpha$	0.975	0.975 (0.003)	0.975 (0.002)	0.951 (0.007)	--
$p_1$	0.8	0.800 (0.016)	0.797 (0.012)	0.723 (0.013)	0.727 (0.012)
$p_2$	0.8	0.799 (0.018)	0.797 (0.014)	0.626 (0.028)	0.727 (0.013)
$p_3$	0.8	0.800 (0.019)	0.797 (0.014)	0.492 (0.047)	0.726 (0.014)
$p_4$	0.8	0.799 (0.015)	0.796 (0.012)	0.492 (0.068)	0.726 (0.011)
$p_5$	0.8	0.801 (0.018)	0.797 (0.015)	0.734 (0.115)	0.726 (0.014)
$c_2$	--	--	--	0.780 (0.016)	--
$c_3$	--	--	--	0.779 (0.014)	--
$c_4$	--	--	--	0.771 (0.012)	--
$c_5$	--	--	--	0.759 (0.015)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		5.00	3.16	53.75	100.40
$N$	1000	998 (3)	998 (2)	1023 (74)	1000 (1)
$\alpha$	1.000	1.000 (0.001)	1.000 (0.001)	0.999 (0.001)	--
$p_1$	0.8	0.802 (0.015)	0.799 (0.012)	0.785 (0.042)	0.801 (0.012)
$p_2$	0.8	0.803 (0.014)	0.799 (0.014)	0.747 (0.105)	0.801 (0.013)
$p_3$	0.8	0.798 (0.015)	0.796 (0.012)	0.640 (0.190)	0.798 (0.012)
$p_4$	0.8	0.802 (0.015)	0.798 (0.012)	0.479 (0.290)	0.800 (0.012)
$p_5$	0.8	0.799 (0.015)	0.797 (0.012)	0.167 (0.213)	0.799 (0.012)
$c_2$	--	--	--	0.801 (0.014)	--
$c_3$	--	--	--	0.798 (0.012)	--
$c_4$	--	--	--	0.801 (0.013)	--
$c_5$	--	--	--	0.799 (0.011)	--
no. not conv.		0	0	6	0
$\sqrt{\text{MSE}(\hat{N})}$		3.60	2.82	77.49	1.00

Table 2.17: [Simulation 3: case 2] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	198 (7)	205 (7)	248 (18)	520 (24)
$\alpha$	0.7	0.696 (0.018)	0.710 (0.017)	0.569 (0.046)	--
$p_1$	0.8	0.797 (0.054)	0.789 (0.043)	0.366 (0.019)	0.308 (0.019)
$p_2$	0.8	0.810 (0.052)	0.788 (0.043)	0.355 (0.024)	0.309 (0.017)
$p_3$	0.8	0.801 (0.051)	0.788 (0.042)	0.396 (0.041)	0.308 (0.018)
$p_4$	0.8	0.799 (0.062)	0.787 (0.044)	0.528 (0.066)	0.308 (0.019)
$p_5$	0.8	0.794 (0.053)	0.777 (0.044)	0.993 (0.014)	0.305 (0.019)
$c_2$	--	--	--	0.578 (0.071)	--
$c_3$	--	--	--	0.564 (0.046)	--
$c_4$	--	--	--	0.542 (0.052)	--
$c_5$	--	--	--	0.495 (0.058)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		7.28	8.60	51.26	320.89
$N$	200	200 (4)	205 (4)	245 (12)	385 (17)
$\alpha$	0.8	0.799 (0.016)	0.807 (0.015)	0.677 (0.032)	--
$p_1$	0.8	0.798 (0.043)	0.784 (0.035)	0.443 (0.026)	0.415 (0.024)
$p_2$	0.8	0.799 (0.040)	0.787 (0.037)	0.385 (0.044)	0.416 (0.024)
$p_3$	0.8	0.798 (0.041)	0.784 (0.034)	0.396 (0.042)	0.415 (0.023)
$p_4$	0.8	0.798 (0.037)	0.782 (0.036)	0.513 (0.080)	0.415 (0.020)
$p_5$	0.8	0.799 (0.041)	0.780 (0.033)	0.937 (0.138)	0.414 (0.024)
$c_2$	--	--	--	0.648 (0.048)	--
$c_3$	--	--	--	0.643 (0.036)	--
$c_4$	--	--	--	0.616 (0.043)	--
$c_5$	--	--	--	0.576 (0.041)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	6.40	46.57	185.77
$N$	200	199 (3)	201 (3)	226 (5)	286 (9)
$\alpha$	0.9	0.897 (0.012)	0.899 (0.011)	0.800 (0.026)	--
$p_1$	0.8	0.806 (0.036)	0.793 (0.032)	0.571 (0.027)	0.562 (0.029)
$p_2$	0.8	0.801 (0.034)	0.787 (0.032)	0.462 (0.041)	0.558 (0.026)
$p_3$	0.8	0.800 (0.038)	0.786 (0.030)	0.431 (0.064)	0.557 (0.027)
$p_4$	0.8	0.803 (0.037)	0.790 (0.032)	0.517 (0.071)	0.559 (0.028)
$p_5$	0.8	0.801 (0.037)	0.790 (0.032)	0.946 (0.049)	0.560 (0.026)
$c_2$	--	--	--	0.720 (0.038)	--
$c_3$	--	--	--	0.711 (0.034)	--
$c_4$	--	--	--	0.705 (0.033)	--
$c_5$	--	--	--	0.677 (0.035)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	3.16	26.47	86.46

Table 2.17 (continued.)

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
<i>N</i>	200	199 (2)	200 (2)	217 (4)	241 (6)
$\alpha$	0.950	0.949 (0.008)	0.949 (0.008)	0.901 (0.022)	--
<i>p</i> <sub>1</sub>	0.8	0.801 (0.042)	0.791 (0.032)	0.663 (0.029)	0.664 (0.029)
<i>p</i> <sub>2</sub>	0.8	0.802 (0.035)	0.791 (0.029)	0.544 (0.053)	0.665 (0.027)
<i>p</i> <sub>3</sub>	0.8	0.801 (0.038)	0.789 (0.030)	0.446 (0.085)	0.664 (0.029)
<i>p</i> <sub>4</sub>	0.8	0.799 (0.037)	0.787 (0.029)	0.510 (0.111)	0.663 (0.027)
<i>p</i> <sub>5</sub>	0.8	0.797 (0.039)	0.785 (0.029)	0.868 (0.094)	0.662 (0.031)
<i>c</i> <sub>2</sub>	--	--	--	0.762 (0.034)	--
<i>c</i> <sub>3</sub>	--	--	--	0.759 (0.030)	--
<i>c</i> <sub>4</sub>	--	--	--	0.746 (0.030)	--
<i>c</i> <sub>5</sub>	--	--	--	0.724 (0.033)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	2.00	17.46	41.43
<i>N</i>	200	199 (2)	199 (2)	210 (3)	220 (4)
$\alpha$	0.975	0.974 (0.006)	0.973 (0.006)	0.948 (0.017)	--
<i>p</i> <sub>1</sub>	0.8	0.805 (0.037)	0.794 (0.030)	0.726 (0.031)	0.730 (0.031)
<i>p</i> <sub>2</sub>	0.8	0.800 (0.034)	0.789 (0.029)	0.621 (0.067)	0.724 (0.028)
<i>p</i> <sub>3</sub>	0.8	0.799 (0.039)	0.787 (0.027)	0.504 (0.113)	0.723 (0.028)
<i>p</i> <sub>4</sub>	0.8	0.802 (0.034)	0.790 (0.028)	0.502 (0.159)	0.725 (0.030)
<i>p</i> <sub>5</sub>	0.8	0.800 (0.037)	0.792 (0.031)	0.714 (0.165)	0.727 (0.028)
<i>c</i> <sub>2</sub>	--	--	--	0.780 (0.031)	--
<i>c</i> <sub>3</sub>	--	--	--	0.776 (0.029)	--
<i>c</i> <sub>4</sub>	--	--	--	0.772 (0.031)	--
<i>c</i> <sub>5</sub>	--	--	--	0.762 (0.030)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	2.23	10.44	20.39
<i>N</i>	200	199 (1)	199 (1)	208 (43)	200 (1)
$\alpha$	1.000	0.999 (0.002)	0.999 (0.001)	0.999 (0.002)	--
<i>p</i> <sub>1</sub>	0.8	0.807 (0.036)	0.793 (0.028)	0.784 (0.076)	0.804 (0.028)
<i>p</i> <sub>2</sub>	0.8	0.805 (0.033)	0.793 (0.028)	0.745 (0.155)	0.804 (0.026)
<i>p</i> <sub>3</sub>	0.8	0.804 (0.028)	0.790 (0.025)	0.701 (0.277)	0.800 (0.025)
<i>p</i> <sub>4</sub>	0.8	0.808 (0.035)	0.793 (0.031)	0.425 (0.427)	0.804 (0.031)
<i>p</i> <sub>5</sub>	0.8	0.796 (0.036)	0.784 (0.029)	0.222 (0.361)	0.794 (0.030)
<i>c</i> <sub>2</sub>	--	--	--	0.806 (0.032)	--
<i>c</i> <sub>3</sub>	--	--	--	0.800 (0.025)	--
<i>c</i> <sub>4</sub>	--	--	--	0.806 (0.030)	--
<i>c</i> <sub>5</sub>	--	--	--	0.796 (0.029)	--
no. not conv.		0	0	4	0
$\sqrt{\text{MSE}(\hat{N})}$		1.41	1.41	43.73	1.00

Table 2.18: [Simulation 3: case 3] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1046 (175)	960 (138)	1121 (117)	2216 (99)
$\alpha$	0.7	0.708 (0.052)	0.694 (0.044)	0.677 (0.063)	--
$p_1$	0.3	0.291 (0.051)	0.320 (0.050)	0.180 (0.014)	0.135 (0.009)
$p_2$	0.3	0.297 (0.058)	0.324 (0.053)	0.190 (0.017)	0.136 (0.009)
$p_3$	0.3	0.298 (0.058)	0.323 (0.054)	0.204 (0.022)	0.136 (0.009)
$p_4$	0.3	0.296 (0.053)	0.324 (0.050)	0.226 (0.030)	0.136 (0.008)
$p_5$	0.3	0.295 (0.052)	0.324 (0.052)	0.257 (0.044)	0.136 (0.008)
$c_2$	--	--	--	0.213 (0.031)	--
$c_3$	--	--	--	0.207 (0.027)	--
$c_4$	--	--	--	0.201 (0.024)	--
$c_5$	--	--	--	0.199 (0.027)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		180.94	143.68	168.31	1220.02
$N$	1000	1036 (150)	963 (107)	1245 (149)	1654 (61)
$\alpha$	0.8	0.810 (0.048)	0.794 (0.038)	0.779 (0.053)	--
$p_1$	0.3	0.292 (0.044)	0.317 (0.037)	0.188 (0.014)	0.181 (0.010)
$p_2$	0.3	0.296 (0.043)	0.319 (0.036)	0.189 (0.018)	0.183 (0.011)
$p_3$	0.3	0.295 (0.043)	0.318 (0.037)	0.191 (0.024)	0.181 (0.010)
$p_4$	0.3	0.293 (0.043)	0.317 (0.036)	0.196 (0.028)	0.181 (0.010)
$p_5$	0.3	0.295 (0.043)	0.319 (0.036)	0.208 (0.033)	0.182 (0.010)
$c_2$	--	--	--	0.247 (0.034)	--
$c_3$	--	--	--	0.239 (0.025)	--
$c_4$	--	--	--	0.234 (0.022)	--
$c_5$	--	--	--	0.228 (0.021)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		154.25	113.21	286.75	656.83
$N$	1000	1019 (113)	980 (93)	1344 (175)	1276 (32)
$\alpha$	0.9	0.906 (0.041)	0.896 (0.036)	0.883 (0.049)	--
$p_1$	0.3	0.299 (0.034)	0.313 (0.031)	0.200 (0.021)	0.236 (0.012)
$p_2$	0.3	0.296 (0.036)	0.311 (0.032)	0.188 (0.025)	0.235 (0.013)
$p_3$	0.3	0.300 (0.037)	0.314 (0.033)	0.180 (0.031)	0.237 (0.012)
$p_4$	0.3	0.298 (0.035)	0.312 (0.031)	0.171 (0.036)	0.235 (0.013)
$p_5$	0.3	0.297 (0.040)	0.311 (0.034)	0.162 (0.041)	0.235 (0.013)
$c_2$	--	--	--	0.276 (0.032)	--
$c_3$	--	--	--	0.274 (0.024)	--
$c_4$	--	--	--	0.267 (0.023)	--
$c_5$	--	--	--	0.263 (0.022)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		114.58	95.12	385.95	277.84

Table 2.18 (continued.)

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	1000	1018 (85)	985 (76)	1425 (314)	1129 (29)
$\alpha$	0.950	0.956 (0.032)	0.947 (0.030)	0.937 (0.039)	--
$p_1$	0.3	0.295 (0.031)	0.307 (0.027)	0.202 (0.032)	0.265 (0.014)
$p_2$	0.3	0.298 (0.031)	0.310 (0.029)	0.188 (0.036)	0.267 (0.015)
$p_3$	0.3	0.297 (0.030)	0.308 (0.028)	0.172 (0.043)	0.266 (0.013)
$p_4$	0.3	0.294 (0.029)	0.308 (0.027)	0.154 (0.046)	0.265 (0.014)
$p_5$	0.3	0.297 (0.031)	0.309 (0.027)	0.141 (0.056)	0.266 (0.014)
$c_2$	--	--	--	0.290 (0.030)	--
$c_3$	--	--	--	0.286 (0.023)	--
$c_4$	--	--	--	0.284 (0.020)	--
$c_5$	--	--	--	0.282 (0.019)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		86.88	77.46	528.41	132.21
$N$	1000	997 (71)	978 (69)	1473 (398)	1065 (22)
$\alpha$	0.975	0.972 (0.027)	0.967 (0.027)	0.957 (0.033)	--
$p_1$	0.3	0.304 (0.026)	0.312 (0.026)	0.206 (0.043)	0.283 (0.014)
$p_2$	0.3	0.301 (0.027)	0.310 (0.026)	0.187 (0.051)	0.281 (0.014)
$p_3$	0.3	0.306 (0.029)	0.313 (0.026)	0.171 (0.058)	0.284 (0.014)
$p_4$	0.3	0.302 (0.026)	0.311 (0.026)	0.152 (0.070)	0.282 (0.015)
$p_5$	0.3	0.302 (0.030)	0.311 (0.029)	0.134 (0.084)	0.282 (0.016)
$c_2$	--	--	--	0.298 (0.033)	--
$c_3$	--	--	--	0.297 (0.021)	--
$c_4$	--	--	--	0.295 (0.022)	--
$c_5$	--	--	--	0.294 (0.022)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		71.06	72.42	618.16	68.62
$N$	1000	971 (39)	960 (44)	1644 (823)	997 (16)
$\alpha$	1.000	0.990 (0.017)	0.986 (0.018)	0.976 (0.026)	--
$p_1$	0.3	0.310 (0.021)	0.314 (0.022)	0.200 (0.055)	0.300 (0.016)
$p_2$	0.3	0.313 (0.023)	0.318 (0.023)	0.182 (0.061)	0.304 (0.016)
$p_3$	0.3	0.311 (0.021)	0.316 (0.022)	0.159 (0.064)	0.302 (0.016)
$p_4$	0.3	0.308 (0.019)	0.314 (0.020)	0.132 (0.068)	0.300 (0.017)
$p_5$	0.3	0.310 (0.022)	0.315 (0.023)	0.116 (0.078)	0.301 (0.015)
$c_2$	--	--	--	0.310 (0.030)	--
$c_3$	--	--	--	0.306 (0.023)	--
$c_4$	--	--	--	0.310 (0.021)	--
$c_5$	--	--	--	0.308 (0.020)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		48.60	59.46	1045.01	16.27

Table 2.19: [Simulation 3: case 4] Non-evolving natural tags 1 with constant capture probability. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE1_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE1_t$		Model L&B $_t$	Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	243 (107)	186 (57)	293 (58)	445 (55)
$\alpha$	0.7	0.744 (0.131)	0.704 (0.088)	0.705 (0.132)	--
$p_1$	0.3	0.291 (0.115)	0.362 (0.101)	0.180 (0.025)	0.137 (0.022)
$p_2$	0.3	0.284 (0.108)	0.361 (0.099)	0.186 (0.028)	0.136 (0.019)
$p_3$	0.3	0.296 (0.119)	0.367 (0.102)	0.202 (0.039)	0.138 (0.021)
$p_4$	0.3	0.286 (0.106)	0.359 (0.095)	0.217 (0.048)	0.136 (0.019)
$p_5$	0.3	0.293 (0.119)	0.369 (0.105)	0.253 (0.070)	0.139 (0.022)
$c_2$	--	--	--	0.205 (0.074)	--
$c_3$	--	--	--	0.204 (0.059)	--
$c_4$	--	--	--	0.199 (0.051)	--
$c_5$	--	--	--	0.200 (0.050)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		115.31	58.69	109.60	251.09
$N$	200	212 (57)	183 (39)	271 (149)	332 (31)
$\alpha$	0.8	0.813 (0.091)	0.793 (0.068)	0.784 (0.103)	--
$p_1$	0.3	0.297 (0.085)	0.352 (0.077)	0.184 (0.033)	0.181 (0.025)
$p_2$	0.3	0.303 (0.090)	0.354 (0.081)	0.184 (0.036)	0.182 (0.028)
$p_3$	0.3	0.298 (0.085)	0.352 (0.072)	0.183 (0.036)	0.181 (0.026)
$p_4$	0.3	0.302 (0.085)	0.354 (0.079)	0.193 (0.048)	0.182 (0.026)
$p_5$	0.3	0.300 (0.089)	0.353 (0.075)	0.200 (0.054)	0.181 (0.024)
$c_2$	--	--	--	0.244 (0.072)	--
$c_3$	--	--	--	0.245 (0.053)	--
$c_4$	--	--	--	0.233 (0.058)	--
$c_5$	--	--	--	0.229 (0.043)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		58.24	42.54	165.05	135.59
$N$	200	208 (35)	188 (28)	292 (165)	257 (16)
$\alpha$	0.9	0.908 (0.068)	0.891 (0.058)	0.880 (0.086)	--
$p_1$	0.3	0.303 (0.074)	0.339 (0.063)	0.193 (0.033)	0.236 (0.031)
$p_2$	0.3	0.298 (0.070)	0.342 (0.061)	0.186 (0.040)	0.238 (0.026)
$p_3$	0.3	0.296 (0.072)	0.339 (0.067)	0.170 (0.045)	0.236 (0.033)
$p_4$	0.3	0.291 (0.062)	0.332 (0.057)	0.162 (0.056)	0.232 (0.029)
$p_5$	0.3	0.300 (0.065)	0.341 (0.064)	0.161 (0.079)	0.238 (0.029)
$c_2$	--	--	--	0.277 (0.061)	--
$c_3$	--	--	--	0.278 (0.055)	--
$c_4$	--	--	--	0.264 (0.044)	--
$c_5$	--	--	--	0.269 (0.052)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		35.90	30.46	188.91	59.20

Table 2.19 (continued.)

		Model NE1 <sub>t</sub>		Model L&B <sub>t</sub>	Model M <sub>t</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$	conditional $\mathcal{L}$
$N$	200	201 (28)	188 (25)	299 (114)	225 (13)
$\alpha$	0.950	0.952 (0.053)	0.938 (0.047)	0.934 (0.063)	--
$p_1$	0.3	0.299 (0.061)	0.334 (0.061)	0.199 (0.044)	0.266 (0.034)
$p_2$	0.3	0.304 (0.065)	0.335 (0.061)	0.184 (0.051)	0.267 (0.035)
$p_3$	0.3	0.300 (0.060)	0.335 (0.056)	0.165 (0.057)	0.267 (0.034)
$p_4$	0.3	0.304 (0.057)	0.336 (0.056)	0.156 (0.066)	0.267 (0.033)
$p_5$	0.3	0.304 (0.061)	0.335 (0.054)	0.140 (0.075)	0.267 (0.031)
$c_2$	--	--	--	0.292 (0.071)	--
$c_3$	--	--	--	0.294 (0.050)	--
$c_4$	--	--	--	0.284 (0.050)	--
$c_5$	--	--	--	0.285 (0.041)	--
no. not conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		28.01	27.73	150.98	28.17
$N$	200	194 (21)	185 (20)	371 (448)	211 (9)
$\alpha$	0.975	0.963 (0.046)	0.955 (0.042)	0.937 (0.061)	--
$p_1$	0.3	0.317 (0.057)	0.340 (0.051)	0.194 (0.054)	0.286 (0.035)
$p_2$	0.3	0.316 (0.057)	0.344 (0.051)	0.177 (0.055)	0.289 (0.028)
$p_3$	0.3	0.312 (0.061)	0.340 (0.054)	0.152 (0.060)	0.285 (0.038)
$p_4$	0.3	0.309 (0.047)	0.333 (0.047)	0.132 (0.051)	0.280 (0.031)
$p_5$	0.3	0.315 (0.053)	0.343 (0.052)	0.114 (0.056)	0.288 (0.032)
$c_2$	--	--	--	0.309 (0.063)	--
$c_3$	--	--	--	0.311 (0.054)	--
$c_4$	--	--	--	0.296 (0.041)	--
$c_5$	--	--	--	0.308 (0.046)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		21.84	25	479.52	14.21
$N$	200	187 (18)	180 (18)	448 (740)	201 (8)
$\alpha$	1.000	0.970 (0.039)	0.966 (0.038)	0.958 (0.050)	--
$p_1$	0.3	0.325 (0.048)	0.348 (0.045)	0.194 (0.068)	0.302 (0.035)
$p_2$	0.3	0.325 (0.051)	0.347 (0.046)	0.172 (0.075)	0.300 (0.031)
$p_3$	0.3	0.329 (0.055)	0.352 (0.053)	0.152 (0.075)	0.305 (0.034)
$p_4$	0.3	0.323 (0.054)	0.342 (0.046)	0.129 (0.079)	0.296 (0.034)
$p_5$	0.3	0.326 (0.052)	0.346 (0.051)	0.116 (0.101)	0.300 (0.034)
$c_2$	--	--	--	0.317 (0.061)	--
$c_3$	--	--	--	0.326 (0.053)	--
$c_4$	--	--	--	0.307 (0.046)	--
$c_5$	--	--	--	0.312 (0.042)	--
no. not conv.		0	0	1	0
$\sqrt{\text{MSE}(\hat{N})}$		22.20	26.90	780.45	8.06

in Simulations 1 and 2 (relative bias < 72% and relative standard errors < 54%, compared to the results in Simulations 1 and 2 where relative bias < 133% and relative standard errors < 212%). However, the estimates varied when data were analyzed under Model L&B<sub>t</sub>, and the estimates were poor (relative bias ≤ 124% and relative standard error ≤ 370%) compared to the estimates from Model L&B<sub>0</sub>.

#### 2.5.4 Simulation 4: Estimated Generalized Least Squares Method

In previous simulations, we examined two methods of estimation under Model NE1<sub>t</sub>, unweighted least squares and minimum  $\chi^2$ , both of which are based on the idea of using the observed values and expected values of  $\mathbf{X}_\gamma$  in a quadratic distance function. The quadratic distance function, in general, has the form

$$\mathcal{F} = (\mathbf{x}_\gamma - \mathbf{E}[\mathbf{X}_\gamma])' \mathbf{C}^{-1} (\mathbf{x}_\gamma - \mathbf{E}[\mathbf{X}_\gamma])$$

(Lindsay and Qu, 2003). The method of unweighted least squares treats  $\mathbf{C}$  as an identity matrix, thus  $\mathbf{C}$  is free of parameters, whereas the method of minimum  $\chi^2$  treats  $\mathbf{C}$  as a diagonal matrix where the diagonal elements of  $\mathbf{C}^{-1}$  are based on the inverse of expected values. In this section, we derive the variance-covariance matrix  $\mathbf{C}$  of the observed capture histories  $\mathbf{X}_\gamma$ , and considered an estimated generalized least squares method (W. Link, personal communication). With this approach, the dependencies in the data are incorporated in the estimator, and this may help to improve precision, especially for the low capture probability cases. For simplicity, we consider cases with  $K = 3$  sampling occasions because the details are unwieldy for  $K > 3$ .

To construct the variance-covariance matrix,  $\mathbf{C}$ , consider only real capture histories for now. The real capture history, given each true capture history, is denoted by  $\delta$ , and the corresponding random variable,  $Z_\delta$ , denotes the number of real capture histories conditional on the true capture history. Note that the  $Z_\delta$  cannot be observed, but represent latent variables. Because the capture history [000] is not observed, we condition on the total number of real capture histories other than [000]. Then, for the 3-sample case, we have 26 distinct real capture histories  $\delta$  (Table 2.20). Here we use letters A to Z to denote each  $\delta$  rather than a sequence of 0's and 1's because the same real capture history can arise from different true capture histories. Each  $\delta$  has its own probability, which is denoted by  $\pi_\delta$ . Now, notice that  $Z_\delta$  is multinomial because we do not consider ghost

Table 2.20: A summary of the latent capture histories,  $\delta$ , and associated probabilities for non-evolving natural tags 1 for the 3-sample case.

$\omega$ (true history)	$\gamma$ (observed history)	status	$\delta$ (latent history)	$\pi_\delta = \Pr[\delta   \omega]$
111	111	real	A	$[p_1\alpha p_2\alpha p_3\alpha]/\pi^*$
	110	real	B	$[p_1\alpha p_2\alpha p_3(1-\alpha)]/\pi^*$
	001	ghost*		
	101	real	C	$[p_1\alpha p_2(1-\alpha)p_3\alpha]/\pi^*$
	010	ghost*		
	011	real	D	$[p_1(1-\alpha)p_2\alpha p_3\alpha]/\pi^*$
	100	ghost*		
	100	real	E	$[p_1\alpha p_2(1-\alpha)p_3(1-\alpha)]/\pi^*$
	010	ghost*		
	001	ghost*		
	010	real	F	$[p_1(1-\alpha)p_2\alpha p_3(1-\alpha)]/\pi^*$
	100	ghost*		
	001	ghost*		
	001	real	G	$[p_1(1-\alpha)p_2(1-\alpha)p_3\alpha]/\pi^*$
	100	ghost*		
	010	ghost*		
000	real	H	$[p_1(1-\alpha)p_2(1-\alpha)p_3(1-\alpha)]/\pi^*$	
100	ghost*			
010	ghost*			
001	ghost*			
110	110	real	I	$[p_1\alpha p_2\alpha(1-p_3)]/\pi^*$
	100	real	J	$[p_1\alpha p_2(1-\alpha)(1-p_3)]/\pi^*$
	010	ghost*		
	010	real	K	$[p_1(1-\alpha)p_2\alpha(1-p_3)]/\pi^*$
	100	ghost*		
	000	real	L	$[p_1(1-\alpha)p_2(1-\alpha)(1-p_3)]/\pi^*$
	100	ghost*		
010	ghost*			

Table 2.20 (continued.)

$\omega$ (true history)	$\gamma$ (observed history)	status	$\delta$ (latent history)	$\pi_\delta = \Pr[\delta   \omega]$
101	101	real	M	$[p_1\alpha(1-p_2)p_3\alpha]/\pi^*$
	100	real	N	$[p_1\alpha(1-p_2)p_3(1-\alpha)]/\pi^*$
	001	ghost*		
	001	real	O	$[p_1(1-\alpha)(1-p_2)p_3\alpha]/\pi^*$
	100	ghost*		
	000	real	P	$[p_1(1-\alpha)(1-p_2)p_3(1-\alpha)]/\pi^*$
	100	ghost*		
	001	ghost*		
	100	100	real	Q
000		real	R	$[p_1(1-\alpha)(1-p_2)(1-p_3)]/\pi^*$
100		ghost*		
011	011	real	S	$[(1-p_1)p_2\alpha p_3\alpha]/\pi^*$
	010	real	T	$[(1-p_1)p_2\alpha p_3(1-\alpha)]/\pi^*$
	001	ghost*		
	001	real	U	$[(1-p_1)p_2(1-\alpha)p_3\alpha]/\pi^*$
	010	ghost*		
	000	real	V	$[(1-p_1)p_2(1-\alpha)p_3(1-\alpha)]/\pi^*$
	010	ghost*		
	001	ghost*		
	010	010	real	W
000		real	X	$[(1-p_1)p_2(1-\alpha)(1-p_3)]/\pi^*$
010		ghost*		
001	001	real	Y	$[(1-p_1)(1-p_2)p_3\alpha]/\pi^*$
	000	real	Z	$[(1-p_1)(1-p_2)p_3(1-\alpha)]/\pi^*$
	001	ghost*		

where  $\pi^* = 1 - (1-p_1)(1-p_2)(1-p_3)$

capture histories here, and the total number of real capture histories, excluding [000], corresponds to the total number of animals captured,  $M_{t+1}$ , thus

$$\mathbf{Z}_\delta \sim \text{multinomial} (M_{t+1}, \pi_\delta).$$

Note that  $M_{t+1}$  is unobservable here. Then, the expected values and variance-covariance of  $\mathbf{Z}_\delta$  can be easily constructed. For the 3-sample case, the expected value of  $\mathbf{Z}_\delta$  is

$$E[\mathbf{Z}_\delta] = M_{t+1} \begin{bmatrix} \pi_A \\ \pi_B \\ \pi_C \\ \vdots \\ \pi_X \\ \pi_Y \\ \pi_Z \end{bmatrix},$$

and the variance-covariance of  $\mathbf{Z}_\delta$  is

$$\text{Var}[\mathbf{Z}_\delta] = M_{t+1} \begin{bmatrix} \pi_A(1 - \pi_A) & -\pi_A\pi_B & \cdots & -\pi_A\pi_Y & -\pi_A\pi_Z \\ -\pi_B\pi_A & \pi_B(1 - \pi_B) & \cdots & -\pi_B\pi_Y & -\pi_B\pi_Z \\ -\pi_C\pi_A & -\pi_C\pi_B & \cdots & -\pi_C\pi_Y & -\pi_C\pi_Z \\ \vdots & \vdots & \ddots & \vdots & \vdots \\ -\pi_X\pi_A & -\pi_X\pi_B & \cdots & -\pi_X\pi_Y & -\pi_X\pi_Z \\ -\pi_Y\pi_A & -\pi_Y\pi_B & \cdots & \pi_Y(1 - \pi_Y) & -\pi_Y\pi_Z \\ -\pi_Z\pi_A & -\pi_Z\pi_B & \cdots & -\pi_Z\pi_Y & \pi_Z(1 - \pi_Z) \end{bmatrix}.$$

Recall that this latent variable  $\mathbf{Z}_\delta$  cannot be observed directly. Similarly,  $M_{t+1}$  is unknown here. However, the expected value of  $M_{t+1}$  can be written in terms of the total number of observed capture histories  $X_{all}$  as



Then, we can write a quadratic distance function

$$\mathcal{F}_{cov} = (\mathbf{x}_\gamma - \mathbf{E}[\mathbf{X}_\gamma])' \mathbf{C}^{-1} (\mathbf{x}_\gamma - \mathbf{E}[\mathbf{X}_\gamma]) ,$$

where

$$\mathbf{E}[\mathbf{X}_\gamma] = \mathbf{W} \mathbf{E}[\mathbf{Z}_\delta]$$

and

$$\mathbf{C} = \mathbf{W} \text{Var}[\mathbf{Z}_\delta] \mathbf{W}' .$$

Then, estimates are obtained by minimizing the quadratic distance function,  $\mathcal{F}_{cov}$ .

In this simulation, we modified the four specific cases described in Simulation 1 by limiting to  $K = 3$  sampling occasions because of the complexity of the elements of  $\mathbf{Z}_\delta$  and  $\mathbf{W}$ .

$$\text{Case 1: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7]$$

$$\text{Case 2: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7]$$

$$\text{Case 3: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3]$$

$$\text{Case 4: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3]$$

For each case, the correct identification rates of  $\alpha = 0.7, 0.8$  and  $0.9$  were considered. Because we were primarily interested in whether accounting for the covariance structure of the data improves the estimates, for each generated data set, estimates were obtained by using three different estimation methods under Model NE1<sub>t</sub>: (1) unweighted least squares ( $\mathcal{F}_{ls}$ ), (2) minimum  $\chi^2$  ( $\mathcal{F}_{\chi^2}$ ) and (3) estimated generalized least squares ( $\mathcal{F}_{cov}$ ). The performance of each estimation method was investigated by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  over 100 simulations. The results for cases 1 to 4 are summarized in Tables 2.21 and 2.22.

We were interested in whether estimates obtained by using different estimation methods differ, especially in cases with high misidentification rates. However, it is clear from the results that the estimates did not improve when the covariance structure of the data was incorporated into the estimator. This is most likely because the elements of  $\mathbf{C}$  were estimated rather than known. Although extending to the 5-sample case may show some improvement, we did not see any advantage with the more complicated estimator in our simulation of the 3-sample case.

Table 2.21: [Simulation 4: cases 1 and 2] Non-evolving natural tags 1. Average estimates (with standard errors in parentheses) based on 100 simulated data sets under Model NE1<sub>t</sub>.

		least squares	minimum $\chi^2$	EGLS**
$N$	1000	1011 (86)	1011 (84)	1010 (84)
$\alpha$	0.7	0.700 (0.027)	0.700 (0.027)	0.700 (0.027)
$p_1$	0.7	0.698 (0.058)	0.698 (0.058)	0.698 (0.058)
$p_2$	0.8	0.796 (0.068)	0.795 (0.065)	0.796 (0.066)
$p_3$	0.7	0.697 (0.059)	0.697 (0.059)	0.697 (0.058)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		86.70	84.71	84.59
$N$	1000	999 (57)	1000 (58)	1000 (58)
$\alpha$	0.8	0.799 (0.021)	0.799 (0.021)	0.799 (0.021)
$p_1$	0.7	0.702 (0.043)	0.702 (0.042)	0.702 (0.043)
$p_2$	0.8	0.805 (0.050)	0.804 (0.051)	0.804 (0.050)
$p_3$	0.7	0.704 (0.041)	0.704 (0.041)	0.703 (0.041)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		57.00	58.00	58.00
$N$	1000	999 (40)	999 (39)	999 (39)
$\alpha$	0.9	0.900 (0.016)	0.899 (0.016)	0.900 (0.016)
$p_1$	0.7	0.700 (0.030)	0.700 (0.030)	0.700 (0.030)
$p_2$	0.8	0.802 (0.033)	0.802 (0.033)	0.802 (0.033)
$p_3$	0.7	0.702 (0.032)	0.702 (0.031)	0.702 (0.031)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		40.01	39.01	39.01
$N$	200	215 (41)	214 (41)	214 (41)
$\alpha$	0.7	0.717 (0.061)	0.717 (0.060)	0.716 (0.060)
$p_1$	0.7	0.673 (0.116)	0.674 (0.116)	0.677 (0.116)
$p_2$	0.8	0.765 (0.129)	0.768 (0.130)	0.770 (0.129)
$p_3$	0.7	0.672 (0.111)	0.674 (0.112)	0.676 (0.112)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		43.65	43.32	43.32
$N$	200	200 (22)	199 (22)	199 (22)
$\alpha$	0.8	0.798 (0.043)	0.796 (0.043)	0.796 (0.043)
$p_1$	0.7	0.708 (0.084)	0.711 (0.087)	0.711 (0.084)
$p_2$	0.8	0.808 (0.090)	0.812 (0.090)	0.812 (0.089)
$p_3$	0.7	0.707 (0.084)	0.710 (0.084)	0.711 (0.084)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		22.00	22.02	22.02
$N$	200	200 (18)	199 (18)	200 (18)
$\alpha$	0.9	0.901 (0.038)	0.900 (0.039)	0.901 (0.039)
$p_1$	0.7	0.705 (0.072)	0.705 (0.073)	0.704 (0.072)
$p_2$	0.8	0.802 (0.073)	0.801 (0.076)	0.801 (0.074)
$p_3$	0.7	0.701 (0.066)	0.701 (0.068)	0.700 (0.067)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		18.00	18.02	18.00

\*\* EGLS = estimated generalized least squares

Table 2.22: [Simulation 4: cases 3 and 4] Non-evolving natural tags 1. Average estimates (with standard errors in parentheses) based on 100 simulated data sets under Model NE1<sub>t</sub>.

		least squares	minimum $\chi^2$	EGLS**
$N$	1000	1176 (641)	1162 (582)	1157 (584)
$\alpha$	0.7	0.729 (0.186)	0.731 (0.173)	0.729 (0.174)
$p_1$	0.3	0.340 (0.176)	0.329 (0.159)	0.332 (0.161)
$p_2$	0.2	0.229 (0.121)	0.220 (0.108)	0.222 (0.109)
$p_3$	0.3	0.340 (0.179)	0.329 (0.164)	0.332 (0.166)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		664.72	604.12	604.73
$N$	1000	1104 (422)	1092 (416)	1090 (418)
$\alpha$	0.8	0.821 (0.153)	0.819 (0.153)	0.818 (0.153)
$p_1$	0.3	0.320 (0.138)	0.322 (0.136)	0.324 (0.137)
$p_2$	0.2	0.214 (0.096)	0.216 (0.095)	0.217 (0.095)
$p_3$	0.3	0.323 (0.139)	0.325 (0.137)	0.326 (0.138)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		434.62	426.05	427.57
$N$	1000	1018 (253)	1017 (250)	1016 (251)
$\alpha$	0.9	0.900 (0.106)	0.900 (0.106)	0.900 (0.106)
$p_1$	0.3	0.320 (0.093)	0.319 (0.094)	0.320 (0.094)
$p_2$	0.2	0.211 (0.065)	0.212 (0.066)	0.212 (0.066)
$p_3$	0.3	0.315 (0.092)	0.316 (0.093)	0.316 (0.093)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		253.63	250.57	251.50
$N$	200	264 (170)	270 (159)	268 (160)
$\alpha$	0.7	0.747 (0.234)	0.771 (0.234)	0.767 (0.238)
$p_1$	0.3	0.376 (0.283)	0.366 (0.281)	0.374 (0.288)
$p_2$	0.2	0.264 (0.198)	0.254 (0.194)	0.260 (0.199)
$p_3$	0.3	0.374 (0.277)	0.360 (0.273)	0.368 (0.279)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		181.64	173.72	173.85
$N$	200	203 (124)	198 (112)	196 (113)
$\alpha$	0.8	0.767 (0.212)	0.776 (0.209)	0.770 (0.213)
$p_1$	0.3	0.438 (0.279)	0.437 (0.278)	0.448 (0.284)
$p_2$	0.2	0.295 (0.188)	0.298 (0.189)	0.305 (0.193)
$p_3$	0.3	0.437 (0.274)	0.441 (0.280)	0.451 (0.286)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		124.03	112.01	113.07
$N$	200	201 (75)	199 (72)	198 (73)
$\alpha$	0.9	0.881 (0.159)	0.883 (0.157)	0.880 (0.160)
$p_1$	0.3	0.362 (0.197)	0.362 (0.194)	0.367 (0.201)
$p_2$	0.2	0.239 (0.129)	0.243 (0.134)	0.246 (0.135)
$p_3$	0.3	0.363 (0.189)	0.362 (0.184)	0.367 (0.189)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		75.00	72.00	73.02

\*\* EGLS = estimated generalized least squares

## 2.6 Discussion

In general, the performance of least squares and minimum  $\chi^2$  estimators under Model NE1<sub>t</sub> was good. The problematic cases are the ones with low capture probabilities, where substantial bias in  $\hat{N}$  can occur, especially as the value of  $\alpha$  approaches 1. Differences between the unweighted least squares and minimum  $\chi^2$  estimators of  $N$  were small, and it was an interesting observation that generalized least squares estimator with estimated variance-covariance did not perform better than these simpler methods.

An important observation is that even when the chance of error is only 0.05, the estimator of  $N$  showed substantial positive bias when misidentification is ignored, and the conventional  $M_t$  estimator is used. This is reasonable because the conventional capture-recapture models do not account for misidentification so that each observed capture history is treated as if it belongs to a distinct animal. Thus, a ghost capture history is also counted as if it belongs to an animal in the population, which leads to overestimation of  $N$ . The magnitude of this bias can be substantial as the misidentification rate increases, and researchers should be aware of the possibility of misidentification and its consequences when their studies use natural tags.

For the cases of relatively low correct identification rates, it is clear that the NE1<sub>t</sub> estimators perform better than the  $M_t$  estimator, as demonstrated by the results from Simulation 1. The results from Simulation 2 also indicated that the NE1<sub>t</sub> estimators also perform well compared to the  $M_t$  estimator when the correct identification rate is as high as 0.975, especially for high capture probability cases. However, as the correct identification rate approaches 1, the performance of the NE1<sub>t</sub> estimators deteriorates, especially for low capture probability cases, whereas the performance of the  $M_t$  estimator improves. These models make different assumptions about the data, and it is not an easy task to determine which is the most appropriate for a given data set. An important topic for future research is to develop a tool to test whether, for a given data set, the true correct identification rate is 1 or close enough to 1 so that misidentification can be ignored. Also, guidelines or criteria that determine whether to use Model NE1 or conventional capture-recapture models need to be developed.

Performance of the maximum likelihood estimator based on the L&B likelihood is poor compared to the estimators based on Model NE1. Although Lukacs and Burnham (2005a) considered only constant capture probability and correct identification rates of 0.95 to 0.99 in their simula-

tion, we considered cases with capture probabilities varied across sampling occasions in addition to the cases with constant capture probability, and used a range of correct identification rates that included values from  $\alpha = 0.7$  to 1.000, where  $\alpha = 1.000$  indicates no misidentification. Estimates under Model L&B<sub>t</sub> are sensitive to starting values, and it is difficult to assess the performance of the estimator. We also note that the number of parameters in Model L&B is larger than that in Model NE1, and that there appears to be a problem with identifiability of Model L&B when we assume time dependent capture probabilities. We tested a few of our generated data sets by imposing the constraint  $p_4 = p_5$  or  $p_5 = c_5$  and also by using program MARK to obtain the L&B<sub>t</sub> estimates. The results from program MARK, as well as our results, support the conclusion that there is an identifiability problem. Both Model NE1 and Model L&B were developed for genetic tag-based capture-recapture studies under the same assumptions about the misidentification mechanism. However, Lukacs and Burnham (2005a) constructed their model based on a multinomial likelihood approach, which we believe to be invalid, whereas we enumerated all possible observed histories and corresponding probabilities. Our estimation methods were based on quadratic distance function, which compared observed and expected numbers of capture histories. We here clearly see differences between Model NE1 and Model L&B, and it is an important next step to understand the differences clearly.

Finally, we have assumed that only a single source of DNA (e.g., a hair sample) of a captured animal at a sampling occasion is analyzed and used to construct capture history data. Thus, at most, only one ghost capture history can be created for each captured animal. In reality, it is more likely to collect multiple sources of DNA for an individual animal at a sampling occasion (i.e., an animal leaves multiple hair samples at a sampling occasion). In such cases, we can recognize that the multiple samples of a captured animal actually belong to the same animal only if the identification based on DNA fingerprints is correct. Thus, those identified correctly are recorded as a single real capture history whereas those that are incorrectly identified are all recorded as separate ghost capture histories. In other words, multiple ghost capture histories can be created for each captured animal at a sampling occasion. Consequently, the capture-recapture data are likely to contain 'extra' ghost capture histories. Such extra ghost capture histories are not considered under Model NE1 developed in this chapter, and we expect even larger bias in  $\hat{N}$  if such extra ghost capture histories are present in the data, but ignored. This multiple capture problem needs to be investigated further, and study designs to reduce observations of extra ghost capture histories

or capture-recapture models that allow extra ghost capture histories need to be considered.

In Chapter 3, we further consider the misidentification mechanism (NE1) discussed in this chapter. We first consider an alternative estimator which is based on the likelihood conditioning on the capture histories that have more than one capture event. Second, we consider an extension of Model NE1 to allow for both behavioral response as well as misidentification. Finally, we discuss augmentation of data, with the goal of improving estimator performance by obtaining extra data on the misidentification rate.

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## Chapter 3

# Extensions of Model NE1

### 3.1 Introduction

In this chapter, we extend Model NE1 illustrated in Chapter 2. First, we consider an alternative estimation method. One of the interesting characteristics of NE1 is that ghost capture histories appear only in the observable capture histories with a single capture event (see Table 2.3). In other words, if we use a subset of the data that includes only capture histories that have two or more capture events, we can eliminate all ghost capture histories, and thus the complex dependency between real and ghost histories. In the first part of this chapter, we focus on this subset of the data, develop a likelihood-based estimator, and perform a simulation study to assess the performance of the estimator.

Variation in the capture probability is a common phenomenon in capture-recapture studies. Variation can occur among individual animals (heterogeneity), across time (temporal), between unmarked and marked animals (behavioral response), or some combination of these, and conventional capture-recapture models have been developed to allow for these types of variation in the capture probabilities (Otis et al., 1978; Pollock et al., 1990; Williams et al., 2002). In the second part of this chapter, we consider a modification of Model NE1 that allows for both misidentification and behavioral response to occur in the same study.

In the last part of this chapter, we extend Model NE1 to incorporate additional external information on the misidentification rate. The basic idea here is similar to the *multi-tube approach* (Navidi et al., 1992; Taberlet et al., 1996; Taberlet and Luikart, 1999; Taberlet et al., 1999), which

performs multiple independent amplifications of DNA. This approach allows for detection of possible genotyping errors by comparing the results of multiple amplifications performed independently, and an accurate genotype can be deduced by examining all of the amplification results. Here we apply a similar idea to the identification procedure. We are interested in the consistency in identification when multiple identifications were performed from a sample that contains an animal's DNA. In other words, if a source of DNA is analyzed independently multiple times, the identification based on the DNA fingerprints should indicate the same animal. However, if misidentification occurs for some reason, we observe inconsistency in the identifications. Such data can provide valuable information for estimating the misidentification rate, as well as for improving the estimation of population size, when they are used to augment the capture history data. We refer to this approach as the *multiple identification*, and we will illustrate the concept by using a simple example, develop an estimator that incorporates such data, and perform a simulation study to assess the estimator performance.

## 3.2 Likelihood-Based Estimation Method

### 3.2.1 Statistical Model Development and Estimation

Here we consider the case of non-evolving natural tags 1 (NE1). In Chapter 2, we defined the observable capture histories  $\gamma$ , and demonstrated the construction of the probability of observing each capture history  $\gamma$  for a study with this type of misidentification. We also presented the marginal probability of each observable capture history (Table 2.3). Recall that, with NE1, "ghosts" do not have a possibility of recapture, and thus every ghost capture history has only a single capture event. Consequently, capture histories that have two or more capture events are all "real". We focus on this feature of the data, and construct a likelihood function by conditioning on the total number of animals that have been captured at least twice. Estimators are then obtained by maximum likelihood.

To give a simple concrete example, consider the 3-sample closed population case we illustrated in Chapter 2. Here we just consider observable capture histories that have two or more capture events, which are denoted by  $\gamma''$  (Table 3.1). The corresponding random variable, which is the number of capture histories that have capture history  $\gamma''$ , is denoted by  $X_{\gamma''}$ , and the total number

Table 3.1: A summary of the probabilities of the observable capture histories under Model NE1<sub>t</sub> conditional on the capture histories that have two or more capture events,  $\gamma''$ , in a 3-sample study.

$\gamma$	$\Pr[\gamma]$	status	$\gamma''$	$\Pr[\gamma''   x''_{all}]$
111	$P'_1 P'_2 P'_3$	real	111	$P'_1 P'_2 P'_3 / \tau^*$
110	$P'_1 P'_2 Q'_3$	real	110	$P'_1 P'_2 Q'_3 / \tau^*$
101	$P'_1 Q'_2 P'_3$	real	101	$P'_1 Q'_2 P'_3 / \tau^*$
100	$P'_1 Q'_2 Q'_3 + p_1(1 - \alpha)$	real + ghost	--	--
011	$Q'_1 P'_2 P'_3$	real	011	$Q'_1 P'_2 P'_3 / \tau^*$
010	$Q'_1 P'_2 Q'_3 + p_2(1 - \alpha)$	real + ghost	--	--
001	$Q'_1 Q'_2 P'_3 + p_3(1 - \alpha)$	real + ghost	--	--
000	$Q'_1 Q'_2 Q'_3$	real	--	--
Total	$1 + (p_1 + p_2 + p_3)(1 - \alpha)$			1

of capture histories that have two or more capture events is denoted by  $x''_{all}$ . Then the probability of observing  $\gamma''$  conditional on  $x''_{all}$ , which is denoted by  $\tau_{\gamma''}$ , can be written as

$$\begin{aligned} \tau_{111} &= \Pr[111 | x''_{all}] = \frac{\Pr[111]}{\tau^*} = \frac{P'_1 P'_2 P'_3}{\tau^*} \\ \tau_{110} &= \Pr[110 | x''_{all}] = \frac{\Pr[110]}{\tau^*} = \frac{P'_1 P'_2 Q'_3}{\tau^*} \\ \tau_{101} &= \Pr[101 | x''_{all}] = \frac{\Pr[101]}{\tau^*} = \frac{P'_1 Q'_2 P'_3}{\tau^*} \\ \tau_{011} &= \Pr[011 | x''_{all}] = \frac{\Pr[011]}{\tau^*} = \frac{Q'_1 P'_2 P'_3}{\tau^*} \end{aligned}$$

where

$$\tau^* = P'_1 P'_2 P'_3 + P'_1 P'_2 Q'_3 + P'_1 Q'_2 P'_3 + Q'_1 P'_2 P'_3.$$

Notice that all  $\gamma''$  are real capture histories, and  $\mathbf{X}_{\gamma''}$  is multinomial,

$$\mathbf{X}_{\gamma''} \sim \text{multinomial} (x''_{all}, \tau_{\gamma''}) .$$

Then the conditional likelihood is

$$\mathcal{L}_c(\mathbf{P}'_i | \mathbf{x}_{\gamma''}, x''_{all}) = \binom{x''_{all}}{x_{111} \ x_{110} \ x_{101} \ x_{011}} [\tau_{111}]^{x_{111}} [\tau_{110}]^{x_{110}} [\tau_{101}]^{x_{101}} [\tau_{011}]^{x_{011}} ,$$

and the estimates are obtained by maximizing  $\mathcal{L}_c$ . Notice that, in  $\mathcal{L}_c$ , the parameters for the capture probabilities ( $p_i$ ) and correct identification rate ( $\alpha$ ) always occur together as a product ( $P'_i = p_i \alpha$ ;  $Q'_i = 1 - P'_i$ ), and we estimate the product  $P'_i$ . We cannot obtain individual estimates of  $p_i$  and  $\alpha$  from the conditional likelihood,  $\mathcal{L}_c$ . However, the estimates of  $P'_i$  are used to estimate  $\tau^*$ , and thus population size is estimated as a derived parameter

$$\hat{N}_c = \frac{x''_{all}}{\hat{\tau}^*} .$$

The estimator  $\hat{N}_c$  is a consistent estimator for  $N$  when misidentification occurs.

For  $K > 3$ , the same principles apply. In general, the probability of observing  $\gamma''$  can be written as

$$\tau_{\gamma''} = \Pr[\gamma'' | x''_{all}] = \frac{\Pr[\gamma]}{\tau^*}$$

where

$$\tau^* = \sum_{\gamma''} \Pr[\gamma] ,$$

and the likelihood function, conditioning on the capture histories that have two or more capture events, is

$$\mathcal{L}_c(\mathbf{P}'_i | \mathbf{x}_{\gamma''}, x''_{all}) = \binom{x''_{all}}{\mathbf{x}_{\gamma''}} \prod_{\gamma''} [\tau_{\gamma''}]^{x_{\gamma''}}$$

where  $x_{\gamma''}$  and  $x''_{all}$  represent the data. The estimate of population size is obtained as a derived parameter shown above.

### 3.2.2 Simulation Study: Conditional Likelihood Estimation Method

The data sets that were generated in Simulation 1 in Chapter 2 are used here to evaluate the conditional maximum likelihood estimator. For each data set, only the capture histories that have two or more capture events were needed for this simulation study. Thus, we have the same four specific cases, each with correct identification rates of  $\alpha = 0.7, 0.8$  and  $0.9$ .

$$\text{Case 1: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 2: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 3: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$$

$$\text{Case 4: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$$

We considered the estimation method based on the conditional likelihood,  $\mathcal{L}_c$ , as illustrated in the previous section, and the estimates of  $P'_i$  were obtained by maximizing  $\mathcal{L}_c$ . Then the estimate of  $N$  was obtained as a derived parameter. The performance of the estimator was assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  based on 100 simulated data sets, and if the estimation process failed to converge, those estimates were excluded from the computation of the results. The results for cases 1 to 4 are summarized in Tables 3.2 - 3.5. In order to compare the performance of the likelihood-based estimator with the other estimators under Model NE1, the results from methods of unweighted least squares and minimum  $\chi^2$  (Tables 2.4 - 2.7) are presented again in Tables 3.2 - 3.5.

For the high capture probability cases, the overall performance of the likelihood-based estimator was good (relative bias  $< 1\%$  and relative standard error  $\leq 5\%$ ), and the bias and precision of  $\hat{N}_c$  were similar to those from unweighted least squares and minimum  $\chi^2$  examined in Simulation 1 in Chapter 2. For case 3, the overall performance of the likelihood-based estimator was also good (relative bias  $< 4\%$  and relative standard error  $< 23\%$ ), and the magnitude of bias in  $\hat{N}_c$  was smaller than those from unweighted least squares and minimum  $\chi^2$ . However, the likelihood-based estimator  $\hat{N}_c$  was more precise than the unweighted least squares estimator, but less precise than the minimum  $\chi^2$  estimator. For case 4,  $\hat{N}_c$  was less precise (relative standard error  $> 35\%$ ) compared to the results from unweighted least squares and minimum  $\chi^2$ . However, the bias in  $\hat{N}_c$  (relative bias  $\approx 6 - 47\%$ ) was not consistently better nor consistently worse compared to the results from unweighted least squares and minimum  $\chi^2$ .

Table 3.2: [Simulation Study: case 1]  $NE1_t$  with likelihood-based estimation method. Average estimates (with standard errors in parentheses) under Model  $NE1_t$ . Estimates are based on 100 simulated data sets.

		NE1 <sub>t</sub>				NE1 <sub>t</sub>
		least squares	minimum $\chi^2$			conditional $\mathcal{L}$
$N$	1000	1000 (21)	1007 (21)	$N$	1000	1000 (21)
$\alpha$	0.7	0.700 (0.008)	0.703 (0.008)	--	--	--
$p_1$	0.7	0.700 (0.026)	0.697 (0.022)	$P'_1$	0.49	0.490 (0.018)
$p_2$	0.8	0.797 (0.027)	0.795 (0.022)	$P'_2$	0.56	0.560 (0.020)
$p_3$	0.7	0.698 (0.027)	0.695 (0.024)	$P'_3$	0.49	0.489 (0.019)
$p_4$	0.8	0.800 (0.026)	0.795 (0.023)	$P'_4$	0.56	0.559 (0.019)
$p_5$	0.7	0.699 (0.025)	0.698 (0.019)	$P'_5$	0.49	0.492 (0.016)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		21.00	22.13	$\sqrt{\text{MSE}(\hat{N})}$		21.00
$N$	1000	999 (13)	1004 (12)	$N$	1000	999 (12)
$\alpha$	0.8	0.799 (0.008)	0.801 (0.008)	--	--	--
$p_1$	0.7	0.700 (0.020)	0.697 (0.017)	$P'_1$	0.56	0.559 (0.017)
$p_2$	0.8	0.798 (0.021)	0.798 (0.017)	$P'_2$	0.64	0.642 (0.014)
$p_3$	0.7	0.698 (0.021)	0.696 (0.018)	$P'_3$	0.56	0.558 (0.018)
$p_4$	0.8	0.801 (0.020)	0.796 (0.016)	$P'_4$	0.64	0.638 (0.016)
$p_5$	0.7	0.701 (0.021)	0.700 (0.020)	$P'_5$	0.56	0.561 (0.018)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		13.03	12.64	$\sqrt{\text{MSE}(\hat{N})}$		12.04
$N$	1000	1000 (8)	1002 (7)	$N$	1000	1000 (7)
$\alpha$	0.9	0.899 (0.005)	0.900 (0.005)	--	--	--
$p_1$	0.7	0.701 (0.018)	0.698 (0.016)	$P'_1$	0.63	0.629 (0.017)
$p_2$	0.8	0.803 (0.016)	0.798 (0.015)	$P'_2$	0.72	0.721 (0.015)
$p_3$	0.7	0.700 (0.019)	0.699 (0.016)	$P'_3$	0.63	0.630 (0.016)
$p_4$	0.8	0.799 (0.015)	0.797 (0.014)	$P'_4$	0.72	0.720 (0.014)
$p_5$	0.7	0.701 (0.018)	0.698 (0.017)	$P'_5$	0.63	0.630 (0.016)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		8.00	7.28	$\sqrt{\text{MSE}(\hat{N})}$		7.00

Table 3.3: [Simulation Study: case 2]  $NE1_t$  with likelihood-based estimation method. Average estimates (with standard errors in parentheses) under Model  $NE1_t$ . Estimates are based on 100 simulated data sets.

		NE1 <sub>t</sub>				NE1 <sub>t</sub>	
		least squares	minimum $\chi^2$			conditional $\mathcal{L}$	
$N$	200	198 (10)	205 (9)	$N$	200	198 (10)	
$\alpha$	0.7	0.695 (0.018)	0.710 (0.018)		--	--	
$p_1$	0.7	0.707 (0.059)	0.700 (0.050)	$P'_1$	0.49	0.497 (0.044)	
$p_2$	0.8	0.806 (0.068)	0.790 (0.049)	$P'_2$	0.56	0.564 (0.043)	
$p_3$	0.7	0.691 (0.053)	0.688 (0.047)	$P'_3$	0.49	0.491 (0.045)	
$p_4$	0.8	0.808 (0.059)	0.786 (0.051)	$P'_4$	0.56	0.557 (0.041)	
$p_5$	0.7	0.703 (0.061)	0.690 (0.046)	$P'_5$	0.49	0.489 (0.042)	
no. not conv.		0	0	no. not conv.		0	
$\sqrt{\text{MSE}(\hat{N})}$		10.19	10.29	$\sqrt{\text{MSE}(\hat{N})}$		10.19	
$N$	200	199 (6)	204 (7)	$N$	200	199 (6)	
$\alpha$	0.8	0.799 (0.018)	0.808 (0.017)		--	--	
$p_1$	0.7	0.702 (0.050)	0.691 (0.037)	$P'_1$	0.56	0.562 (0.036)	
$p_2$	0.8	0.794 (0.041)	0.782 (0.042)	$P'_2$	0.64	0.642 (0.038)	
$p_3$	0.7	0.702 (0.051)	0.691 (0.043)	$P'_3$	0.56	0.559 (0.038)	
$p_4$	0.8	0.805 (0.049)	0.784 (0.042)	$P'_4$	0.64	0.641 (0.038)	
$p_5$	0.7	0.706 (0.045)	0.696 (0.041)	$P'_5$	0.56	0.567 (0.040)	
no. not conv.		0	0	no. not conv.		0	
$\sqrt{\text{MSE}(\hat{N})}$		6.08	8.06	$\sqrt{\text{MSE}(\hat{N})}$		6.08	
$N$	200	199 (4)	202 (3)	$N$	200	199 (3)	
$\alpha$	0.9	0.900 (0.013)	0.903 (0.012)		--	--	
$p_1$	0.7	0.703 (0.036)	0.693 (0.032)	$P'_1$	0.63	0.630 (0.034)	
$p_2$	0.8	0.806 (0.038)	0.787 (0.034)	$P'_2$	0.72	0.721 (0.034)	
$p_3$	0.7	0.705 (0.041)	0.693 (0.031)	$P'_3$	0.63	0.633 (0.035)	
$p_4$	0.8	0.798 (0.035)	0.785 (0.033)	$P'_4$	0.72	0.719 (0.035)	
$p_5$	0.7	0.690 (0.038)	0.682 (0.034)	$P'_5$	0.63	0.621 (0.036)	
no. not conv.		0	0	no. not conv.		0	
$\sqrt{\text{MSE}(\hat{N})}$		4.12	3.60	$\sqrt{\text{MSE}(\hat{N})}$		3.16	

Table 3.4: [Simulation Study: case 3]  $NE1_t$  with likelihood-based estimation method. Average estimates (with standard errors in parentheses) under Model  $NE1_t$ . Estimates are based on 100 simulated data sets.

		$NE1_t$				$NE1_t$
		least squares	minimum $\chi^2$			conditional $\mathcal{L}$
$N$	1000	1034 (225)	916 (169)	$N$	1000	1028 (222)
$\alpha$	0.7	0.704 (0.069)	0.680 (0.056)	--	--	--
$p_1$	0.3	0.303 (0.065)	0.340 (0.060)	$P'_1$	0.21	0.210 (0.030)
$p_2$	0.2	0.203 (0.048)	0.230 (0.045)	$P'_2$	0.14	0.139 (0.022)
$p_3$	0.3	0.303 (0.069)	0.340 (0.062)	$P'_3$	0.21	0.210 (0.029)
$p_4$	0.2	0.205 (0.048)	0.232 (0.045)	$P'_4$	0.14	0.142 (0.026)
$p_5$	0.3	0.303 (0.067)	0.340 (0.061)	$P'_5$	0.21	0.210 (0.029)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		227.55	188.72	$\sqrt{\text{MSE}(\hat{N})}$		223.75
$N$	1000	1048 (209)	946 (165)	$N$	1000	1031 (206)
$\alpha$	0.8	0.813 (0.073)	0.788 (0.062)	--	--	--
$p_1$	0.3	0.297 (0.062)	0.330 (0.061)	$P'_1$	0.24	0.241 (0.031)
$p_2$	0.2	0.199 (0.042)	0.223 (0.041)	$P'_2$	0.16	0.161 (0.025)
$p_3$	0.3	0.298 (0.061)	0.330 (0.060)	$P'_3$	0.24	0.239 (0.033)
$p_4$	0.2	0.196 (0.041)	0.221 (0.040)	$P'_4$	0.16	0.160 (0.023)
$p_5$	0.3	0.297 (0.062)	0.329 (0.058)	$P'_5$	0.24	0.240 (0.030)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		214.44	173.61	$\sqrt{\text{MSE}(\hat{N})}$		208.31
$N$	1000	1014 (132)	956 (108)	$N$	1000	1003 (122)
$\alpha$	0.9	0.904 (0.048)	0.889 (0.041)	--	--	--
$p_1$	0.3	0.302 (0.041)	0.321 (0.037)	$P'_1$	0.27	0.272 (0.026)
$p_2$	0.2	0.197 (0.032)	0.214 (0.030)	$P'_2$	0.18	0.181 (0.022)
$p_3$	0.3	0.301 (0.043)	0.320 (0.039)	$P'_3$	0.27	0.273 (0.026)
$p_4$	0.2	0.199 (0.029)	0.214 (0.026)	$P'_4$	0.18	0.180 (0.019)
$p_5$	0.3	0.300 (0.041)	0.319 (0.037)	$P'_5$	0.27	0.270 (0.026)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		132.74	116.61	$\sqrt{\text{MSE}(\hat{N})}$		122.03

Table 3.5: [Simulation Study: case 4]  $NE1_t$  with likelihood-based estimation method. Average estimates (with standard errors in parentheses) under Model  $NE1_t$ . Estimates are based on 100 simulated data sets.

		NE1 <sub>t</sub>				NE1 <sub>t</sub>
		least squares	minimum $\chi^2$			conditional $\mathcal{L}$
$N$	200	258 (120)	185 (94)	$N$	200	293 (383)
$\alpha$	0.7	0.761 (0.159)	0.700 (0.132)	--	--	--
$p_1$	0.3	0.297 (0.159)	0.402 (0.154)	$P'_1$	0.21	0.206 (0.076)
$p_2$	0.2	0.195 (0.107)	0.277 (0.108)	$P'_2$	0.14	0.140 (0.052)
$p_3$	0.3	0.294 (0.159)	0.402 (0.153)	$P'_3$	0.21	0.213 (0.073)
$p_4$	0.2	0.196 (0.108)	0.281 (0.116)	$P'_4$	0.14	0.143 (0.055)
$p_5$	0.3	0.296 (0.160)	0.402 (0.147)	$P'_5$	0.21	0.210 (0.067)
no. not conv.		0	0	no. not conv.		2
$\sqrt{\text{MSE}(\hat{N})}$		133.28	95.18	$\sqrt{\text{MSE}(\hat{N})}$		394.12
$N$	200	221 (75)	170 (48)	$N$	200	213 (81)
$\alpha$	0.8	0.819 (0.122)	0.770 (0.089)	--	--	--
$p_1$	0.3	0.307 (0.120)	0.386 (0.102)	$P'_1$	0.24	0.239 (0.063)
$p_2$	0.2	0.208 (0.085)	0.272 (0.078)	$P'_2$	0.16	0.159 (0.043)
$p_3$	0.3	0.304 (0.119)	0.390 (0.105)	$P'_3$	0.24	0.247 (0.060)
$p_4$	0.2	0.198 (0.076)	0.266 (0.074)	$P'_4$	0.16	0.160 (0.044)
$p_5$	0.3	0.302 (0.118)	0.390 (0.109)	$P'_5$	0.24	0.252 (0.066)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		77.88	56.60	$\sqrt{\text{MSE}(\hat{N})}$		82.03
$N$	200	209 (44)	181 (37)	$N$	200	219 (75)
$\alpha$	0.9	0.906 (0.087)	0.877 (0.081)	--	--	--
$p_1$	0.3	0.302 (0.072)	0.356 (0.075)	$P'_1$	0.27	0.264 (0.055)
$p_2$	0.2	0.202 (0.062)	0.250 (0.066)	$P'_2$	0.18	0.180 (0.047)
$p_3$	0.3	0.302 (0.077)	0.358 (0.082)	$P'_3$	0.27	0.269 (0.063)
$p_4$	0.2	0.202 (0.058)	0.248 (0.064)	$P'_4$	0.18	0.177 (0.048)
$p_5$	0.3	0.295 (0.082)	0.352 (0.084)	$P'_5$	0.27	0.266 (0.058)
no. not conv.		0	0	no. not conv.		0
$\sqrt{\text{MSE}(\hat{N})}$		44.91	41.59	$\sqrt{\text{MSE}(\hat{N})}$		77.36

In general, the results indicate that performance of the conditional maximum likelihood estimator was comparable to the methods that use all of the capture histories, except in cases with low capture probabilities. Conditioning on histories with at least two captures will eliminate a larger fraction of the data when the capture probabilities are low, and as a result, methods of unweighted least squares and minimum  $\chi^2$  will have better properties compared to the conditional maximum likelihood approach.

### 3.3 Model NE1 with Behavioral Responses

#### 3.3.1 Statistical Model Development and Estimation

In this section, we again consider the case of non-evolving natural tags 1 (NE1). Assumptions for the misidentification mechanism we make here are the same as those described in Chapter 2. However, we consider variation in capture probability due to behavioral response. Thus, as for the conventional behavioral response capture-recapture model (Model  $M_b$ ), we have two parameters for capture probability,  $p$  for unmarked animals and  $c$  for marked animals. Also, for simplicity, we assume that the probability of correct identification is constant for all animals at any capture event with a parameter for correct identification rate,  $\alpha$ . The construction of the probabilities of observable capture histories  $\gamma$  is very similar to the case we described in Chapter 2. For example, with the 3-sample case, an animal which is captured at all sampling occasions has true capture history [111], but there are several possible observed capture histories depending on when misidentification occurs. One of the possibilities is the pair [101 ; 010], which is the case where identification at the first and third capture events is correct, but at the second capture event is incorrect. Given that an animal has true capture history [111], the probability of observing the animal with real capture history [101] is  $p\alpha c(1-\alpha)c\alpha$ . The ghost capture history [010] that is created due to misidentification at the second capture event also has the same probability  $p\alpha c(1-\alpha)c\alpha$  because real and ghost capture histories are totally dependent. Table 3.6 presents the probability of all the observable capture histories for the 3-sample case. The marginal probabilities for the observed capture histories for the 3-sample case are also summarized in Table 3.7 where  $q = (1-p)$ ,  $P' = p\alpha$ ,  $Q' = (1-P')$ ,  $C' = c\alpha$ , and  $D' = (1-C')$ . As with the case in Chapter 2, total probability exceeds 1 because of the ghost capture histories created, and it equals 1 if and

only if no misidentification occurs (i.e.,  $\alpha = 1$ ).

For  $K > 3$  cases, the same principles apply. Let  $t_1(\gamma)$  be the sampling occasion when the first capture occurs for a given capture history  $\gamma$ . Then the general expression for the probability of observing capture history  $\gamma$  is

$$\Pr[\gamma] = \left[ (1-p)^{(t_1(\gamma)-1)} P' + h \left( p(1-\alpha) C' \sum_{i=2}^{t_1(\gamma)} (1-p)^{(t_1(\gamma)-i)} (1-C')^{(i-2)} \right) \right] \times \left[ \prod_{i=t_1(\gamma)+1}^K C'^{\gamma_i} (1-C')^{(1-\gamma_i)} \right]$$

for  $\gamma$  with multiple capture events, and

$$\Pr[\gamma] = \left[ (1-p)^{(t_1(\gamma)-1)} P' + h \left( p(1-\alpha) C' \sum_{i=2}^{t_1(\gamma)} (1-p)^{(t_1(\gamma)-i)} (1-C')^{(i-2)} \right) \right] \times \left[ \prod_{i=t_1(\gamma)+1}^K C'^{\gamma_i} (1-C')^{(1-\gamma_i)} \right] + \left[ (1-p)^{(t_1(\gamma)-1)} p + h \left( 1 - (1-p)^{(t_1(\gamma)-1)} \right) c \right] (1-\alpha)$$

for  $\gamma$  with a single capture event, where

$p$  is the capture probability of an unmarked animal

$c$  is the capture probability of an marked animal

$\alpha$  is the probability of correct identification

$P' = p\alpha$

$C' = c\alpha$

$h = 0$  if  $t_1(\gamma) = 1$  ; else  $h = 1$ .

Again, the typical multinomial approach to building a likelihood function for the observed capture histories is invalid because of the dependency between real and ghost histories, and the fact that the total probability exceeds 1. We apply the methods of unweighted least squares and minimum  $\chi^2$ , both of which are based on the idea of using the observed values and marginal expected values of  $\mathbf{X}_\gamma$  to obtain estimates. The marginal expected values of  $\mathbf{X}_\gamma$  for the 3-sample

Table 3.6: A summary of the observable capture histories,  $\gamma$ , and associated probabilities for non-evolving natural tags 1 with behavioral response for the 3-sample case.

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma   \omega]$
111	none	111	real	$pacaca$
		110	real	$pacac(1 - \alpha)$
	at third	001	ghost*	$pacac(1 - \alpha)$
		101	real	$pac(1 - \alpha)c\alpha$
		010	ghost*	$pac(1 - \alpha)c\alpha$
		011	real	$p(1 - \alpha)cac\alpha$
	at first	100	ghost*	$p(1 - \alpha)cac\alpha$
		at second and third	100	real
	010		ghost*	$pac(1 - \alpha)c(1 - \alpha)$
	001		ghost*	$pac(1 - \alpha)c(1 - \alpha)$
	at first and third	010	real	$p(1 - \alpha)cac(1 - \alpha)$
		100	ghost*	$p(1 - \alpha)cac(1 - \alpha)$
		001	ghost*	$p(1 - \alpha)cac(1 - \alpha)$
	at first and second	001	real	$p(1 - \alpha)c(1 - \alpha)c\alpha$
		100	ghost*	$p(1 - \alpha)c(1 - \alpha)c\alpha$
		010	ghost*	$p(1 - \alpha)c(1 - \alpha)c\alpha$
	at first, second and third	000	real	$p(1 - \alpha)c(1 - \alpha)c(1 - \alpha)$
		100	ghost*	$p(1 - \alpha)c(1 - \alpha)c(1 - \alpha)$
		010	ghost*	$p(1 - \alpha)c(1 - \alpha)c(1 - \alpha)$
		001	ghost*	$p(1 - \alpha)c(1 - \alpha)c(1 - \alpha)$
110	none	110	real	$p\alpha c\alpha(1 - c)$
		100	real	$p\alpha c(1 - \alpha)(1 - c)$
	at second	010	ghost*	$p\alpha c(1 - \alpha)(1 - c)$
		010	real	$p(1 - \alpha)c\alpha(1 - c)$
	at first	100	ghost*	$p(1 - \alpha)c\alpha(1 - c)$
		at first and second	000	real
	100		ghost*	$p(1 - \alpha)c(1 - \alpha)(1 - c)$
	010		ghost*	$p(1 - \alpha)c(1 - \alpha)(1 - c)$

Table 3.6 (continued.)

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma   \omega]$
101	none	101	real	$p\alpha(1-c)c\alpha$
		100	real	$p\alpha(1-c)c(1-\alpha)$
	at second	001	ghost*	$p\alpha(1-c)c(1-\alpha)$
		001	real	$p(1-\alpha)(1-c)c\alpha$
		100	ghost*	$p(1-\alpha)(1-c)c\alpha$
	at first and second	000	real	$p(1-\alpha)(1-c)c(1-\alpha)$
		100	ghost*	$p(1-\alpha)(1-c)c(1-\alpha)$
		001	ghost*	$p(1-\alpha)(1-c)c(1-\alpha)$
	100	at none	100	real
at third		000	real	$p(1-\alpha)(1-c)(1-c)$
		100	ghost*	$p(1-\alpha)(1-c)(1-c)$
011	none	011	real	$(1-p)p\alpha c\alpha$
		010	real	$(1-p)p\alpha c(1-\alpha)$
	at third	001	ghost*	$(1-p)p\alpha c(1-\alpha)$
		001	real	$(1-p)p(1-\alpha)c\alpha$
		010	ghost*	$(1-p)p(1-\alpha)c\alpha$
	at second and third	000	real	$(1-p)p(1-\alpha)c(1-\alpha)$
		010	ghost*	$(1-p)p(1-\alpha)c(1-\alpha)$
		001	ghost*	$(1-p)p(1-\alpha)c(1-\alpha)$
	010	none	010	real
at second		000	real	$(1-p)p(1-\alpha)(1-c)$
		010	ghost*	$(1-p)p(1-\alpha)(1-c)$
001	none	001	real	$(1-p)(1-p)p\alpha$
	at third	000	real	$(1-p)(1-p)p(1-\alpha)$
		001	ghost*	$(1-p)(1-p)p(1-\alpha)$
000	none	000	real	$(1-p)(1-p)(1-p)$

Table 3.7: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for non-evolving natural tags 1 with behavioral response in a 3-sample study.

$\gamma$ (observed history)	$\Pr[\gamma]$
111	$P' C' C'$
110	$P' C' D'$
101	$P' D' C'$
100	$P' D' D' + p(1 - \alpha)$
011	$q P' C' + p(1 - \alpha)C'C'$
010	$q P' D' + p(1 - \alpha)C'D' + [qp + (1 - q)c](1 - \alpha)$
001	$q q P' + p(1 - \alpha)D'C' + qp(1 - \alpha)C' + [q^2p + (1 - q^2)c](1 - \alpha)$
000	$q q Q' + p(1 - \alpha)D'D' + qp(1 - \alpha)D'$
Total**	$1 + [(1 + q + q^2)p + ((1 - q) + (1 - q^2))c](1 - \alpha)$

\*\* Total = 1 if and only if  $\alpha = 1$ .

case can be written as a product of population size and the appropriate cell probabilities (Table 3.7),

$$E[X_\gamma] = N\Pr[\gamma] .$$

Then, the estimates are obtained by minimizing the quadratic distance function

$$\mathcal{F}_{ls} = \sum_{\gamma, \gamma \neq 000} (x_\gamma - E[X_\gamma])^2$$

or

$$\mathcal{F}_{\chi^2} = \sum_{\gamma, \gamma \neq 000} \frac{(x_\gamma - E[X_\gamma])^2}{E[X_\gamma]}$$

where  $x_\gamma$  represents the data and  $X_\gamma$  represents the random variable.

The method can also be conditioned on the total number of capture histories observed,  $X_{all}$ .

The total probability associated with the observed capture histories is

$$\begin{aligned}
p^* &= 1 - [qqQ' + p(1 - \alpha)D'D' + qp(1 - \alpha)D'] \\
&\quad + [p + qp + (1 - q)c + q^2p + (1 - q^2)c] (1 - \alpha) \\
&= 1 - [qqQ' + p(1 - \alpha)D'D' + qp(1 - \alpha)D'] \\
&\quad + [(1 + q + q^2)p + ((1 - q) + (1 - q^2))c] (1 - \alpha)
\end{aligned}$$

for the 3-sample study case, or in general,

$$\begin{aligned}
p^* &= 1 - \left[ (1 - p)^{(K-1)}(1 - P') + \sum_{i=0}^{K-2} \left( (1 - p)^i (1 - C')^{(K-i-1)} \right) p(1 - \alpha) \right] \\
&\quad + \left[ \sum_{i=1}^K \left( (1 - p)^{(i-1)} p + \left( 1 - (1 - p)^{(i-1)} \right) c \right) \right] (1 - \alpha)
\end{aligned}$$

for the  $K$ -sample case. Then expected values of  $\mathbf{X}_\gamma$  with the conditional approach can be written as

$$E[X_\gamma | X_{all} = x_{all}] = \frac{x_{all} \Pr[\gamma]}{p^*}$$

where  $x_{all}$  is the total number of capture histories observed. Again, the estimates are obtained by minimizing the quadratic distance function  $\mathcal{F}_{I_s}$  or  $\mathcal{F}_{\chi^2}$  where expectations are conditional on  $x_{all}$ , so that the parameter  $N$  is removed from the estimation process. Then  $N$  is estimated as a derived parameter,

$$\hat{N} = \frac{x_{all}}{\hat{p}^*}.$$

### 3.3.2 Simulation Study: Cases with Behavioral Responses

In this simulation study, we again considered a closed population of  $N$  animals, and a study with  $K = 5$  sampling occasions. Here we have two parameters for capture probabilities,  $p$  for unmarked animals and  $c$  for marked animals, and each unmarked or marked animal was subject to capture with probability  $p$  or  $c$ , respectively, at each sampling occasion. When an animal was captured, identification of the animal was either correct with probability  $\alpha$  or incorrect with probability  $(1 - \alpha)$ . Note that the probability of correct and incorrect identification does not differ between unmarked and marked animals. If the identification was correct, the event was recorded

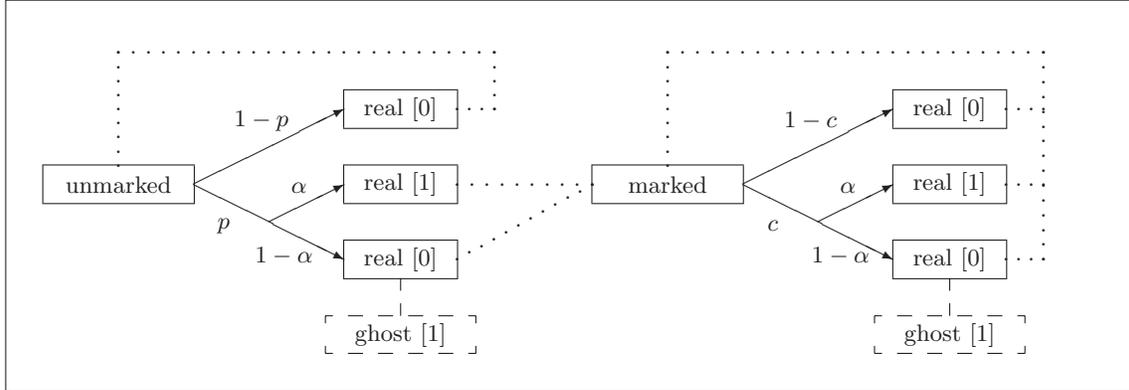


Figure 3.1: A diagram of the misidentification mechanism for non-evolving natural tags 1 with behavioral response.

as a capture (i.e., [1]) in the real capture history of the animal. However, if the identification was incorrect, the event was recorded as a non-capture (i.e., [0]) in the real capture history, and a ghost capture history was created with the event recorded as a capture (i.e., [1]). Then, each animal was subject to capture at the next sampling occasion (see Figure 3.1). Note that a real capture history always has the possibility of recapture. However, a ghost capture history does not have the possibility of recapture, and misidentification always creates a new ghost capture history.

Parameter values were chosen to reflect a wide range of population sizes, capture and recapture probabilities and correct identification rates. We considered the following three specific cases.

$$\text{Case A: } p = 0.8 \quad \text{and} \quad c = 0.5$$

$$\text{Case B: } p = 0.3 \quad \text{and} \quad c = 0.1$$

$$\text{Case C: } p = 0.3 \quad \text{and} \quad c = 0.5$$

Cases A and B describe negative behavioral response with high and low initial capture probabilities, respectively, and case C describes positive behavioral response with a low initial capture probability. We expect that positive behavioral responses would be less problematic, and estimators would have good properties, especially if the initial capture probability is high. Thus, we omit the case with positive behavioral response and high initial capture probability from this simulation study. For each case, population sizes  $N$  of 1000 and 200, and correct identification rates of  $\alpha = 0.7, 0.8,$  and  $0.9$  were considered. We considered unweighted least squares and minimum  $\chi^2$

estimators based on the quadratic distance functions of  $\mathcal{F}_{I_s}$  and  $\mathcal{F}_{\chi^2}$ , respectively. However, we only considered the conditional (on  $x_{all}$ ) approach here. We were also interested in the comparison of estimates obtained under our NE1 model (**Model NE1<sub>b</sub>**) and the corresponding conventional capture-recapture model (**Model M<sub>b</sub>**). Thus, the same generated data sets were analyzed under these two different models.

The performance of the estimators was assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  based on 100 simulated data sets, and if the estimation process failed to converge, those estimates were excluded from the computation of the results. The results for cases A to C are summarized in Tables 3.8 - 3.10. Note that 'convergence' only means that the estimation process successfully reached a local optimum, and it does not necessarily mean that the estimates are reasonable values. Among data sets where the algorithm converged, the estimates from two data sets for case C with  $N = 200$  and  $\alpha = 0.7$  and one data set for case C with  $N = 200$  and  $\alpha = 0.8$  were extremely unrealistic. Thus, these estimates were also excluded from the computation of the results presented in Table 3.10.

Analogous to the cases with time dependent capture probability considered in Chapter 2, the simulation results indicated that  $\hat{N}$  was positively biased when data were analyzed under Model M<sub>b</sub>, and bias in  $\hat{N}$  increased as the misidentification rate increased. However, the bias in  $\hat{N}$  was smaller for the negative behavioral response cases (relative bias  $\approx 10 - 110\%$ ) and much larger for the positive behavioral response cases (relative bias  $\approx 50 - 460\%$ ) compared to those for the cases with time specific capture probabilities (relative bias  $\approx 25 - 155\%$ ). For case A, the performance of NE1<sub>b</sub> estimator was good (relative bias  $\leq 3\%$  and relative standard error  $< 8\%$ ). For case B,  $\hat{N}$  under Model NE1<sub>b</sub> was negatively biased except for cases with  $\alpha = 0.7$  and unweighted least squares, and the estimates were more biased with minimum  $\chi^2$  (relative bias  $> 10\%$ ) than with unweighted least squares (relative bias  $< 8\%$ ). For the exceptional cases that had positive bias in  $\hat{N}$ , there were no obvious outliers. However, there were a number of data sets with  $\hat{\alpha} \approx 1$ , which can lead to an increase in the estimate of population size. This might have caused an increase in the average of  $\hat{N}$ , thus positive bias for the case. For case C, estimators of  $N$  were all positively biased.  $\hat{N}$  from unweighted least squares were more biased and less precise (relative bias  $\approx 0.5 - 21\%$  and relative standard error  $\approx 7 - 70\%$ ) than those from minimum  $\chi^2$  (relative bias  $< 3\%$  and relative standard error  $< 26\%$ ). Note that, for the case with  $N = 200$  and  $\alpha = 0.7$ ,  $\hat{N}$  from unweighted least squares seemed exceptionally biased and less precise. For this case, we observed five relatively

Table 3.8: [Simulation Study: case A] Non-evolving natural tags 1 with behavioral response. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>b</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>b</sub>		Model M <sub>b</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	998 (32)	1005 (24)	2059 (52)
$\alpha$	0.7	0.701 (0.012)	0.704 (0.012)	--
$p$	0.8	0.804 (0.037)	0.797 (0.023)	0.339 (0.011)
$c$	0.5	0.502 (0.023)	0.501 (0.016)	0.216 (0.007)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.06	24.51	1060.27
$N$	1000	996 (20)	1001 (15)	1649 (30)
$\alpha$	0.8	0.799 (0.010)	0.801 (0.009)	--
$p$	0.8	0.804 (0.026)	0.800 (0.018)	0.426 (0.011)
$c$	0.5	0.504 (0.014)	0.504 (0.012)	0.290 (0.008)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		20.39	15.03	649.69
$N$	1000	1001 (17)	1002 (15)	1297 (18)
$\alpha$	0.9	0.901 (0.008)	0.901 (0.008)	--
$p$	0.8	0.798 (0.022)	0.798 (0.017)	0.555 (0.013)
$c$	0.5	0.500 (0.012)	0.500 (0.012)	0.382 (0.009)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		17.02	15.13	297.54
$N$	200	205 (15)	205 (11)	413 (22)
$\alpha$	0.7	0.704 (0.030)	0.714 (0.028)	--
$p$	0.8	0.782 (0.080)	0.788 (0.058)	0.342 (0.023)
$c$	0.5	0.486 (0.050)	0.503 (0.034)	0.214 (0.015)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		15.81	12.08	214.13
$N$	200	203 (11)	206 (9)	329 (15)
$\alpha$	0.8	0.806 (0.027)	0.815 (0.024)	--
$p$	0.8	0.786 (0.069)	0.779 (0.051)	0.429 (0.029)
$c$	0.5	0.494 (0.038)	0.497 (0.032)	0.290 (0.018)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		11.40	10.81	129.86
$N$	200	201 (7)	203 (6)	260 (8)
$\alpha$	0.9	0.901 (0.017)	0.905 (0.015)	--
$p$	0.8	0.792 (0.049)	0.778 (0.041)	0.552 (0.031)
$c$	0.5	0.496 (0.026)	0.497 (0.025)	0.379 (0.019)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	6.70	60.53

Table 3.9: [Simulation Study: case B] Non-evolving natural tags 1 with behavioral response. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>b</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>b</sub>		Model M <sub>b</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1031 (264)	868 (153)	1301 (71)
$\alpha$	0.7	0.765 (0.208)	0.638 (0.109)	--
$p$	0.3	0.318 (0.101)	0.364 (0.067)	0.229 (0.018)
$c$	0.1	0.109 (0.071)	0.147 (0.048)	0.047 (0.004)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		265.81	202.07	309.26
$N$	1000	957 (226)	858 (144)	1195 (52)
$\alpha$	0.8	0.789 (0.176)	0.713 (0.108)	--
$p$	0.3	0.340 (0.102)	0.367 (0.063)	0.250 (0.018)
$c$	0.1	0.125 (0.066)	0.148 (0.043)	0.063 (0.005)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		230.05	202.23	201.81
$N$	1000	928 (178)	889 (128)	1100 (44)
$\alpha$	0.9	0.849 (0.140)	0.820 (0.103)	--
$p$	0.3	0.343 (0.089)	0.350 (0.056)	0.271 (0.019)
$c$	0.1	0.130 (0.058)	0.140 (0.039)	0.081 (0.006)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		192.01	169.42	109.25
$N$	200	213 (66)	167 (53)	259 (27)
$\alpha$	0.7	0.804 (0.223)	0.677 (0.178)	--
$p$	0.3	0.329 (0.159)	0.412 (0.136)	0.234 (0.038)
$c$	0.1	0.114 (0.107)	0.189 (0.104)	0.049 (0.011)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		67.26	62.43	64.88
$N$	200	190 (66)	166 (49)	248 (27)
$\alpha$	0.8	0.771 (0.223)	0.727 (0.167)	--
$p$	0.3	0.372 (0.171)	0.401 (0.133)	0.238 (0.041)
$c$	0.1	0.150 (0.110)	0.191 (0.101)	0.061 (0.010)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		66.75	59.64	55.07
$N$	200	191 (50)	170 (40)	225 (19)
$\alpha$	0.9	0.863 (0.180)	0.805 (0.138)	--
$p$	0.3	0.352 (0.149)	0.383 (0.113)	0.265 (0.036)
$c$	0.1	0.137 (0.092)	0.177 (0.084)	0.079 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		50.80	50.00	31.40

Table 3.10: [Simulation Study: case C] Non-evolving natural tags 1 with behavioral response. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model NE1<sub>b</sub> are from the conditional (on  $x_{all}$ ) approach.

		Model NE1 <sub>b</sub>		Model M <sub>b</sub>
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1005 (148)	998 (99)	4519 (979)
$\alpha$	0.7	0.698 (0.028)	0.703 (0.022)	--
$p$	0.3	0.306 (0.049)	0.308 (0.036)	0.071 (0.017)
$c$	0.5	0.506 (0.051)	0.505 (0.035)	0.219 (0.008)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		148.08	99.02	3652.64
$N$	1000	1005 (93)	1003 (70)	2415 (250)
$\alpha$	0.8	0.799 (0.018)	0.802 (0.016)	--
$p$	0.3	0.302 (0.035)	0.303 (0.028)	0.126 (0.016)
$c$	0.5	0.501 (0.030)	0.502 (0.025)	0.293 (0.010)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		93.13	70.06	1436.91
$N$	1000	1021 (70)	1015 (58)	1508 (80)
$\alpha$	0.9	0.902 (0.015)	0.904 (0.015)	--
$p$	0.3	0.294 (0.029)	0.298 (0.023)	0.198 (0.016)
$c$	0.5	0.496 (0.019)	0.497 (0.019)	0.384 (0.012)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		73.08	59.90	514.26
$N$	200	241 (137)	204 (51)	1111 (899)
$\alpha$	0.7	0.710 (0.072)	0.721 (0.050)	--
$p$	0.3	0.299 (0.112)	0.326 (0.075)	0.076 (0.035)
$c$	0.5	0.502 (0.123)	0.516 (0.077)	0.219 (0.020)
no. not conv.		0	0	4
$\sqrt{\text{MSE}(\hat{N})}$		143.00	51.15	1279.89
$N$	200	213 (50)	205 (32)	511 (123)
$\alpha$	0.8	0.807 (0.042)	0.819 (0.037)	--
$p$	0.3	0.295 (0.071)	0.309 (0.060)	0.124 (0.033)
$c$	0.5	0.503 (0.067)	0.509 (0.057)	0.299 (0.021)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		51.66	32.38	334.43
$N$	200	203 (32)	200 (25)	302 (42)
$\alpha$	0.9	0.900 (0.037)	0.908 (0.032)	--
$p$	0.3	0.310 (0.063)	0.322 (0.053)	0.205 (0.040)
$c$	0.5	0.495 (0.055)	0.498 (0.047)	0.380 (0.023)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.14	25.00	110.30

large estimates where  $\hat{N} > 500$  with unweighted least squares whereas there was no  $\hat{N} > 500$  with minimum  $\chi^2$ . These five estimates inflated the average  $\hat{N}$  and decreased precision.

In general, the performance of the NE1<sub>b</sub> estimators was good when the capture probabilities were high, and the parameters describing the behavioral response and misidentification were reasonably well estimated. When capture probabilities were low, the data did not contain sufficient information for estimating behavioral response and misidentification rate resulting in poor estimation performance. Also, the estimates under Model NE1<sub>b</sub> were better with positive behavioral response than with negative behavioral response as expected.

## 3.4 Supplemental Data from Multiple Identification

### 3.4.1 Statistical Model Development and Estimation

Extra information on the misidentification rate may be used so that estimates may be improved by augmenting the capture history data. This is similar to the idea of tag-return models when a supplemental study is done to learn about the reporting rate. Different study designs can be developed, but the typical augmented study has two components; a standard capture-recapture study component augmented with an extra information component. In this section, we particularly consider application of *multiple identification* to obtain extra information on the misidentification rate, illustrate the concept with a simple study design in which multiple identification is performed only at the last sampling occasion, and then develop a statistical model to analyze such data.

Consider a 3-sample genetic tag-based capture-recapture study. Suppose we perform a standard genetic tag-based capture-recapture study as described in Chapter 2 so that we can construct 3-sample capture-recapture data from identifications based on the DNA fingerprints. We assume there is a risk of misidentification, and that the misidentification mechanism, data structure and statistical model formulation that we described in Chapter 2 apply.

For simplicity, we perform multiple identification on the last sampling occasion only. Suppose that 150 capture histories were observed at the last sampling occasion, and among them 100 capture histories were recaptures (i.e., have at least one capture event before the last sampling occasion). In other words, 100 recapture histories were observed at the last sampling occasion, when the standard capture-recapture study was performed. From these 100 recapture histories

$n^* = 20$  samples are selected for re-analysis. If there are no errors in the DNA fingerprints, animals identified from the first and second analyses should match because they are from the same source of DNA. However, if misidentification occurs for some reason, for example a genotyping error, we observe inconsistency between the identifications.

The key point is that, for the  $n^*$  samples, we perform two identifications on the same sources of DNA. And, for identifications from the first and second DNA fingerprints to be the same, both identifications must be correct. So, choose  $n^*$  randomly from the samples which correspond to histories with two or more captures (i.e., recaptures) because, under the assumptions of NE1, the identifications of the capture histories that have two or more capture events must be correct, and misidentification can be detected in the second analyses if the second DNA fingerprint does not match the first. In a sense, we are creating a known population of  $n^*$  animals, and multiple identification was performed on the known population. Assuming that the laboratory procedures that generate the first and second DNA fingerprints are independent, then the number of consistent identifications or matches, which is denoted as a random variable  $\mathbf{X}^*$ , is binomial

$$\mathbf{X}^* \sim \text{binomial} (n^*, \alpha),$$

and its expected value can be written as  $E[X^*] = n^* \alpha$ .

Combining all data from this specific study design, the conditional (on  $x_{all}$ ) expected values can be written as

$$\begin{aligned} E[X_{111}] &= \frac{x_{all} [P'_1 P'_2 P'_3]}{p^*} \\ E[X_{110}] &= \frac{x_{all} [P'_1 P'_2 Q'_3]}{p^*} \\ E[X_{101}] &= \frac{x_{all} [P'_1 Q'_2 P'_3]}{p^*} \\ E[X_{100}] &= \frac{x_{all} [P'_1 Q'_2 Q'_3 + p_1 (1 - \alpha)]}{p^*} \\ E[X_{011}] &= \frac{x_{all} [Q'_1 P'_2 P'_3]}{p^*} \\ E[X_{010}] &= \frac{x_{all} [Q'_1 P'_2 Q'_3 + p_2 (1 - \alpha)]}{p^*} \\ E[X_{001}] &= \frac{x_{all} [Q'_1 Q'_2 P'_3 + p_3 (1 - \alpha)]}{p^*} \\ E[X^*] &= n^* \alpha \end{aligned}$$

where  $x_{all}$  is the total number of capture histories observed in the standard capture-recapture study component, and

$$p^* = 1 - Q'_1 Q'_2 Q'_3 + (p_1 + p_2 + p_3)(1 - \alpha).$$

Note that the first seven expected values (i.e.,  $E[X_\gamma]$ ) correspond to the standard capture-recapture component and the last one (i.e.,  $E[X^*]$ ) corresponds to the multiple identification component. Then, the estimates are obtained by minimizing the quadratic distance function

$$\mathcal{F}_{ls} = \sum_{\gamma^*} (x_{\gamma^*} - E[X_{\gamma^*}])^2$$

or

$$\mathcal{F}_{\chi^2} = \sum_{\gamma^*} \frac{(x_{\gamma^*} - E[X_{\gamma^*}])^2}{E[X_{\gamma^*}]}$$

where  $x_{\gamma^*}$  represents the augmented data, consisting of the standard capture-recapture component ( $x_\gamma$ ) and the multiple identification component ( $x^*$ ). With this conditional approach, the parameter  $N$  is removed from the estimation process and estimated as a derived parameter,

$$\hat{N} = \frac{x_{all}}{\hat{p}^*}.$$

The same principles apply to studies where  $K > 3$ . We considered the Model NE1<sub>t</sub> developed in Chapter 2 as an example here, but other misidentification models (e.g., Model NE1<sub>b</sub>) can be used for the standard capture-recapture component. Also, we considered a simple study design for the multiple identification component. However, other study designs can be applied, and, if so, the appropriate structure of the statistical model needs to be developed accordingly.

### 3.4.2 Simulation 1: Application of Multiple Identification to NE1<sub>t</sub>

In simulation 1, we considered the application of the multiple identification to Model NE1<sub>t</sub>. We used the data generated for Simulation 1 in Chapter 2 for the standard capture-recapture component of the study ( $x_\gamma$ ), and we have the same specific four cases here.

$$\text{Case 1: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 2: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

Case 3:  $N = 1000$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

Case 4:  $N = 200$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

To generate data for the multiple identification component of the study ( $x^*$ ), we randomly chose  $n^*$  histories from the recaptures at the last sampling occasion, and each of them was assigned either correct identification with probability  $\alpha$  or incorrect identification with probability  $(1 - \alpha)$ . Then the number of capture histories that had the correct identification was counted. For each data set, the values of  $n^* = 20$  and  $40$  were considered to examine whether estimates can be improved by augmenting the capture history data with additional information on the misidentification rate, and how much the degree of improvement differs depending on the sample size used for multiple identification. We also considered estimators obtained assuming that the value of  $\alpha$  is known from external information, that means, with  $\alpha$  fixed at the true value and not estimated during the simulation.

We considered estimation based on the methods of unweighted least squares and minimum  $\chi^2$  that use the quadratic distance functions of  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$ , respectively. We considered only the conditional (on  $x_{all}$ ) approach here. The performance of the estimators was assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  based on 100 simulated data sets, and the model here is denoted as **Model NE1** $_{t,\alpha}$  to indicate that we have extra information on the correct identification rate,  $\alpha$ . The results for cases 1 to 4 are summarized in Tables 3.11 - 3.14. Note that  $n^* = 0$  indicates that the study that did not include any multiple identification, which is the case we examined in Simulation 1 in Chapter 2. Thus, the results for  $n^* = 0$  are exactly the same as those presented in Tables 2.4 - 2.7. However, they are presented again here for comparison purposes.

We here expected less biased and more precise  $\hat{N}$  when capture-recapture data were augmented with extra information on misidentification rate. However, the results indicated that, for high capture probability cases, the estimates based on the quadratic distance functions  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$  were not improved by performing multiple identification. In fact, we observed a number of unexpected results where  $\hat{N}$  was more biased or less precise, especially when the value of  $\alpha$  was assumed to be known. For low capture probability cases, precision of  $\hat{N}$  was always improved by performing multiple identification, and the improvement was always greater when  $n^* = 40$  than with  $n^* = 20$ . The precision was further improved for known  $\alpha$  cases. The bias in  $\hat{N}$  was also reduced in most

Table 3.11: [Simulation 1: case 1] Application of multiple identification to  $NE1_t$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{t,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	1000	1000 (21)	1000 (21)	1000 (21)	1000 (22)
$\alpha$	0.7	0.700 (0.008)	0.700 (0.008)	0.700 (0.008)	--
$p_1$	0.7	0.700 (0.026)	0.700 (0.026)	0.700 (0.026)	0.699 (0.026)
$p_2$	0.8	0.797 (0.027)	0.797 (0.027)	0.797 (0.027)	0.796 (0.026)
$p_3$	0.7	0.698 (0.027)	0.698 (0.027)	0.698 (0.027)	0.698 (0.027)
$p_4$	0.8	0.800 (0.026)	0.800 (0.026)	0.800 (0.026)	0.799 (0.025)
$p_5$	0.7	0.699 (0.025)	0.699 (0.025)	0.699 (0.025)	0.699 (0.024)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		21.00	21.00	21.00	20.00
$N$	1000	999 (13)	999 (13)	999 (13)	1002 (19)
$\alpha$	0.8	0.799 (0.008)	0.799 (0.008)	0.799 (0.008)	--
$p_1$	0.7	0.700 (0.020)	0.700 (0.020)	0.700 (0.020)	0.699 (0.021)
$p_2$	0.8	0.798 (0.021)	0.798 (0.021)	0.798 (0.021)	0.797 (0.021)
$p_3$	0.7	0.698 (0.021)	0.698 (0.021)	0.698 (0.021)	0.697 (0.020)
$p_4$	0.8	0.801 (0.020)	0.801 (0.020)	0.801 (0.020)	0.800 (0.020)
$p_5$	0.7	0.701 (0.021)	0.701 (0.021)	0.701 (0.021)	0.700 (0.022)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		13.03	13.03	13.03	19.10
$N$	1000	1000 (8)	1000 (8)	1000 (8)	1001 (16)
$\alpha$	0.9	0.899 (0.005)	0.899 (0.005)	0.899 (0.005)	--
$p_1$	0.7	0.701 (0.018)	0.701 (0.018)	0.701 (0.018)	0.700 (0.018)
$p_2$	0.8	0.803 (0.016)	0.803 (0.016)	0.803 (0.016)	0.802 (0.017)
$p_3$	0.7	0.700 (0.019)	0.700 (0.019)	0.700 (0.019)	0.700 (0.019)
$p_4$	0.8	0.799 (0.015)	0.799 (0.015)	0.799 (0.015)	0.798 (0.016)
$p_5$	0.7	0.701 (0.018)	0.701 (0.018)	0.701 (0.018)	0.701 (0.019)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		8.00	8.00	8.00	16.03

Table 3.11 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	1000	1007 (21)	1007 (21)	1007 (21)	999 (20)
$\alpha$	0.7	0.703 (0.008)	0.703 (0.008)	0.703 (0.008)	--
$p_1$	0.7	0.697 (0.022)	0.697 (0.022)	0.697 (0.022)	0.700 (0.021)
$p_2$	0.8	0.795 (0.022)	0.795 (0.022)	0.795 (0.022)	0.799 (0.021)
$p_3$	0.7	0.695 (0.024)	0.695 (0.024)	0.695 (0.024)	0.699 (0.022)
$p_4$	0.8	0.795 (0.023)	0.795 (0.023)	0.795 (0.023)	0.799 (0.021)
$p_5$	0.7	0.698 (0.019)	0.698 (0.019)	0.698 (0.019)	0.702 (0.017)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		22.13	22.13	22.13	20.02
$N$	1000	1004 (12)	1004 (12)	1004 (12)	1002 (17)
$\alpha$	0.8	0.801 (0.008)	0.801 (0.008)	0.801 (0.008)	--
$p_1$	0.7	0.697 (0.017)	0.697 (0.017)	0.697 (0.017)	0.698 (0.018)
$p_2$	0.8	0.798 (0.017)	0.798 (0.017)	0.798 (0.017)	0.799 (0.015)
$p_3$	0.7	0.696 (0.018)	0.696 (0.018)	0.696 (0.018)	0.697 (0.018)
$p_4$	0.8	0.796 (0.016)	0.796 (0.016)	0.796 (0.016)	0.797 (0.017)
$p_5$	0.7	0.700 (0.020)	0.700 (0.020)	0.700 (0.020)	0.700 (0.019)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		12.64	12.64	12.64	17.11
$N$	1000	1002 (7)	1002 (7)	1002 (7)	1002 (15)
$\alpha$	0.9	0.900 (0.005)	0.900 (0.005)	0.900 (0.005)	--
$p_1$	0.7	0.698 (0.016)	0.698 (0.016)	0.698 (0.016)	0.698 (0.016)
$p_2$	0.8	0.798 (0.015)	0.798 (0.015)	0.798 (0.015)	0.798 (0.016)
$p_3$	0.7	0.699 (0.016)	0.699 (0.016)	0.699 (0.016)	0.699 (0.016)
$p_4$	0.8	0.797 (0.014)	0.797 (0.014)	0.797 (0.014)	0.797 (0.014)
$p_5$	0.7	0.698 (0.017)	0.698 (0.017)	0.698 (0.017)	0.698 (0.016)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.28	7.28	7.28	15.13

Table 3.12: [Simulation 1: case 2] Application of multiple identification to  $NE1_t$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{t,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	200	198 (10)	198 (10)	198 (10)	201 (10)
$\alpha$	0.7	0.695 (0.018)	0.695 (0.018)	0.695 (0.017)	--
$p_1$	0.7	0.707 (0.059)	0.707 (0.059)	0.707 (0.058)	0.699 (0.058)
$p_2$	0.8	0.806 (0.068)	0.806 (0.068)	0.807 (0.068)	0.796 (0.066)
$p_3$	0.7	0.691 (0.053)	0.691 (0.053)	0.691 (0.053)	0.682 (0.053)
$p_4$	0.8	0.808 (0.059)	0.808 (0.059)	0.808 (0.058)	0.797 (0.052)
$p_5$	0.7	0.703 (0.061)	0.703 (0.061)	0.703 (0.060)	0.695 (0.059)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		10.19	10.19	10.19	10.04
$N$	200	199 (6)	199 (6)	199 (6)	199 (9)
$\alpha$	0.8	0.799 (0.018)	0.799 (0.018)	0.799 (0.017)	--
$p_1$	0.7	0.702 (0.050)	0.702 (0.050)	0.702 (0.050)	0.700 (0.048)
$p_2$	0.8	0.794 (0.041)	0.795 (0.041)	0.794 (0.041)	0.793 (0.042)
$p_3$	0.7	0.702 (0.051)	0.703 (0.051)	0.702 (0.051)	0.701 (0.050)
$p_4$	0.8	0.805 (0.049)	0.805 (0.049)	0.805 (0.048)	0.803 (0.049)
$p_5$	0.7	0.706 (0.045)	0.706 (0.045)	0.706 (0.045)	0.705 (0.047)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		6.08	6.08	6.08	9.05
$N$	200	199 (4)	199 (4)	199 (4)	199 (7)
$\alpha$	0.9	0.900 (0.013)	0.900 (0.012)	0.900 (0.012)	--
$p_1$	0.7	0.703 (0.036)	0.703 (0.036)	0.703 (0.036)	0.703 (0.039)
$p_2$	0.8	0.806 (0.038)	0.806 (0.038)	0.806 (0.038)	0.805 (0.040)
$p_3$	0.7	0.705 (0.041)	0.705 (0.041)	0.705 (0.041)	0.705 (0.045)
$p_4$	0.8	0.798 (0.035)	0.798 (0.035)	0.798 (0.035)	0.797 (0.038)
$p_5$	0.7	0.690 (0.038)	0.690 (0.038)	0.690 (0.038)	0.690 (0.040)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.12	4.12	4.12	7.07

Table 3.12 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	200	205 (9)	205 (9)	205 (9)	200 (9)
$\alpha$	0.7	0.710 (0.018)	0.710 (0.017)	0.710 (0.017)	--
$p_1$	0.7	0.700 (0.050)	0.700 (0.050)	0.700 (0.049)	0.710 (0.047)
$p_2$	0.8	0.790 (0.049)	0.790 (0.050)	0.791 (0.049)	0.802 (0.048)
$p_3$	0.7	0.688 (0.047)	0.688 (0.047)	0.688 (0.047)	0.698 (0.045)
$p_4$	0.8	0.786 (0.051)	0.786 (0.051)	0.786 (0.050)	0.797 (0.044)
$p_5$	0.7	0.690 (0.046)	0.690 (0.046)	0.690 (0.046)	0.701 (0.045)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		10.29	10.29	10.29	9.00
$N$	200	204 (7)	204 (7)	204 (7)	199 (8)
$\alpha$	0.8	0.808 (0.017)	0.808 (0.017)	0.808 (0.017)	--
$p_1$	0.7	0.691 (0.037)	0.691 (0.037)	0.691 (0.037)	0.698 (0.037)
$p_2$	0.8	0.782 (0.042)	0.783 (0.042)	0.783 (0.043)	0.791 (0.041)
$p_3$	0.7	0.691 (0.043)	0.691 (0.043)	0.691 (0.043)	0.697 (0.039)
$p_4$	0.8	0.784 (0.042)	0.784 (0.042)	0.784 (0.042)	0.792 (0.039)
$p_5$	0.7	0.696 (0.041)	0.696 (0.041)	0.696 (0.041)	0.704 (0.042)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		8.06	8.06	8.06	8.06
$N$	200	202 (3)	202 (3)	202 (3)	200 (7)
$\alpha$	0.9	0.903 (0.012)	0.903 (0.012)	0.903 (0.012)	--
$p_1$	0.7	0.693 (0.032)	0.693 (0.032)	0.693 (0.032)	0.695 (0.034)
$p_2$	0.8	0.787 (0.034)	0.787 (0.034)	0.787 (0.034)	0.789 (0.034)
$p_3$	0.7	0.693 (0.031)	0.693 (0.031)	0.693 (0.031)	0.695 (0.034)
$p_4$	0.8	0.785 (0.033)	0.785 (0.033)	0.785 (0.033)	0.787 (0.035)
$p_5$	0.7	0.682 (0.034)	0.682 (0.034)	0.682 (0.034)	0.684 (0.035)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.60	3.60	3.60	7.00

Table 3.13: [Simulation 1: case 3] Application of multiple identification to  $NE1_t$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{t,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	1000	1034 (225)	1014 (176)	1019 (162)	1014 (64)
$\alpha$	0.7	0.704 (0.069)	0.699 (0.056)	0.700 (0.048)	--
$p_1$	0.3	0.303 (0.065)	0.304 (0.055)	0.301 (0.050)	0.296 (0.026)
$p_2$	0.2	0.203 (0.048)	0.204 (0.041)	0.202 (0.038)	0.198 (0.022)
$p_3$	0.3	0.303 (0.069)	0.304 (0.058)	0.301 (0.052)	0.296 (0.027)
$p_4$	0.2	0.205 (0.048)	0.206 (0.042)	0.204 (0.039)	0.200 (0.024)
$p_5$	0.3	0.303 (0.067)	0.305 (0.057)	0.302 (0.051)	0.296 (0.027)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		227.55	176.55	163.11	65.51
$N$	1000	1048 (209)	1033 (180)	1023 (149)	1003 (63)
$\alpha$	0.8	0.813 (0.073)	0.808 (0.064)	0.806 (0.052)	--
$p_1$	0.3	0.297 (0.062)	0.299 (0.056)	0.299 (0.047)	0.300 (0.026)
$p_2$	0.2	0.199 (0.042)	0.200 (0.038)	0.200 (0.032)	0.201 (0.019)
$p_3$	0.3	0.298 (0.061)	0.300 (0.056)	0.300 (0.048)	0.301 (0.027)
$p_4$	0.2	0.196 (0.041)	0.198 (0.037)	0.198 (0.033)	0.198 (0.020)
$p_5$	0.3	0.297 (0.062)	0.299 (0.056)	0.299 (0.047)	0.300 (0.027)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		214.44	183.00	150.76	63.07
$N$	1000	1014 (132)	1013 (125)	1009 (110)	999 (35)
$\alpha$	0.9	0.904 (0.048)	0.904 (0.045)	0.903 (0.040)	--
$p_1$	0.3	0.302 (0.041)	0.301 (0.040)	0.302 (0.036)	0.302 (0.018)
$p_2$	0.2	0.197 (0.032)	0.197 (0.031)	0.197 (0.028)	0.197 (0.018)
$p_3$	0.3	0.301 (0.043)	0.301 (0.041)	0.301 (0.035)	0.300 (0.018)
$p_4$	0.2	0.199 (0.029)	0.198 (0.028)	0.199 (0.027)	0.199 (0.017)
$p_5$	0.3	0.300 (0.041)	0.300 (0.040)	0.301 (0.036)	0.301 (0.021)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		132.74	125.67	110.36	35.01

Table 3.13 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	1000	916 (169)	917 (155)	920 (145)	965 (50)
$\alpha$	0.7	0.680 (0.056)	0.681 (0.051)	0.682 (0.048)	--
$p_1$	0.3	0.340 (0.060)	0.338 (0.055)	0.336 (0.053)	0.314 (0.021)
$p_2$	0.2	0.230 (0.045)	0.228 (0.042)	0.227 (0.040)	0.212 (0.019)
$p_3$	0.3	0.340 (0.062)	0.338 (0.057)	0.336 (0.054)	0.314 (0.023)
$p_4$	0.2	0.232 (0.045)	0.231 (0.042)	0.229 (0.040)	0.214 (0.020)
$p_5$	0.3	0.340 (0.061)	0.338 (0.057)	0.337 (0.055)	0.315 (0.024)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		188.72	175.82	165.60	61.03
$N$	1000	946 (165)	945 (155)	946 (151)	969 (49)
$\alpha$	0.8	0.788 (0.062)	0.788 (0.058)	0.789 (0.056)	--
$p_1$	0.3	0.330 (0.061)	0.329 (0.058)	0.328 (0.056)	0.314 (0.022)
$p_2$	0.2	0.223 (0.041)	0.223 (0.040)	0.222 (0.039)	0.212 (0.017)
$p_3$	0.3	0.330 (0.060)	0.329 (0.057)	0.328 (0.056)	0.314 (0.022)
$p_4$	0.2	0.221 (0.040)	0.221 (0.039)	0.220 (0.037)	0.210 (0.016)
$p_5$	0.3	0.329 (0.058)	0.328 (0.055)	0.328 (0.053)	0.313 (0.022)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		173.61	164.46	160.36	57.98
$N$	1000	956 (108)	956 (104)	957 (100)	979 (31)
$\alpha$	0.9	0.889 (0.041)	0.889 (0.039)	0.890 (0.038)	--
$p_1$	0.3	0.321 (0.037)	0.321 (0.036)	0.320 (0.034)	0.310 (0.016)
$p_2$	0.2	0.214 (0.030)	0.214 (0.029)	0.213 (0.028)	0.206 (0.017)
$p_3$	0.3	0.320 (0.039)	0.320 (0.038)	0.320 (0.036)	0.309 (0.016)
$p_4$	0.2	0.214 (0.026)	0.214 (0.026)	0.214 (0.025)	0.207 (0.014)
$p_5$	0.3	0.319 (0.037)	0.319 (0.036)	0.318 (0.035)	0.308 (0.017)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		116.61	112.92	108.85	37.44

Table 3.14: [Simulation 1: case 4] Application of multiple identification to  $NE1_t$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{t,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	200	258 (120)	214 (64)	208 (52)	204 (27)
$\alpha$	0.7	0.761 (0.159)	0.709 (0.079)	0.703 (0.064)	--
$p_1$	0.3	0.297 (0.159)	0.309 (0.100)	0.312 (0.096)	0.302 (0.052)
$p_2$	0.2	0.195 (0.107)	0.203 (0.069)	0.205 (0.070)	0.199 (0.047)
$p_3$	0.3	0.294 (0.159)	0.303 (0.094)	0.305 (0.085)	0.296 (0.047)
$p_4$	0.2	0.196 (0.108)	0.204 (0.075)	0.205 (0.068)	0.198 (0.042)
$p_5$	0.3	0.296 (0.160)	0.311 (0.115)	0.313 (0.105)	0.302 (0.062)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		133.28	65.51	52.61	27.29
$N$	200	221 (75)	211 (54)	208 (40)	205 (21)
$\alpha$	0.8	0.819 (0.122)	0.805 (0.073)	0.803 (0.053)	--
$p_1$	0.3	0.307 (0.120)	0.305 (0.089)	0.301 (0.074)	0.297 (0.053)
$p_2$	0.2	0.208 (0.085)	0.206 (0.067)	0.203 (0.053)	0.201 (0.040)
$p_3$	0.3	0.304 (0.119)	0.301 (0.086)	0.296 (0.068)	0.293 (0.048)
$p_4$	0.2	0.198 (0.076)	0.198 (0.062)	0.195 (0.053)	0.193 (0.039)
$p_5$	0.3	0.302 (0.118)	0.297 (0.078)	0.293 (0.063)	0.290 (0.041)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		77.88	55.10	40.79	21.58
$N$	200	209 (44)	207 (32)	208 (30)	205 (21)
$\alpha$	0.9	0.906 (0.087)	0.903 (0.060)	0.905 (0.047)	--
$p_1$	0.3	0.302 (0.072)	0.300 (0.062)	0.297 (0.059)	0.300 (0.058)
$p_2$	0.2	0.202 (0.062)	0.198 (0.045)	0.196 (0.043)	0.197 (0.042)
$p_3$	0.3	0.302 (0.077)	0.298 (0.063)	0.296 (0.063)	0.297 (0.055)
$p_4$	0.2	0.202 (0.058)	0.199 (0.047)	0.197 (0.045)	0.198 (0.042)
$p_5$	0.3	0.295 (0.082)	0.289 (0.060)	0.287 (0.056)	0.289 (0.052)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		44.91	32.75	31.04	21.58

Table 3.14 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	200	185 (94)	171 (56)	170 (48)	174 (20)
$\alpha$	0.7	0.700 (0.132)	0.687 (0.086)	0.688 (0.074)	--
$p_1$	0.3	0.402 (0.154)	0.397 (0.124)	0.393 (0.114)	0.363 (0.053)
$p_2$	0.2	0.277 (0.108)	0.273 (0.087)	0.270 (0.079)	0.251 (0.045)
$p_3$	0.3	0.402 (0.153)	0.397 (0.122)	0.392 (0.111)	0.363 (0.053)
$p_4$	0.2	0.281 (0.116)	0.277 (0.097)	0.273 (0.088)	0.253 (0.046)
$p_5$	0.3	0.402 (0.147)	0.399 (0.118)	0.395 (0.109)	0.366 (0.056)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		95.18	63.06	56.60	32.80
$N$	200	170 (48)	171 (41)	171 (36)	182 (15)
$\alpha$	0.8	0.770 (0.089)	0.773 (0.074)	0.775 (0.065)	--
$p_1$	0.3	0.386 (0.102)	0.380 (0.092)	0.375 (0.084)	0.343 (0.044)
$p_2$	0.2	0.272 (0.078)	0.267 (0.072)	0.264 (0.066)	0.241 (0.036)
$p_3$	0.3	0.390 (0.105)	0.383 (0.093)	0.378 (0.086)	0.345 (0.045)
$p_4$	0.2	0.266 (0.074)	0.261 (0.068)	0.258 (0.064)	0.236 (0.037)
$p_5$	0.3	0.390 (0.109)	0.383 (0.097)	0.378 (0.089)	0.343 (0.040)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		56.60	50.21	46.22	23.43
$N$	200	181 (37)	181 (34)	183 (32)	190 (15)
$\alpha$	0.9	0.877 (0.081)	0.879 (0.073)	0.883 (0.068)	--
$p_1$	0.3	0.356 (0.075)	0.353 (0.070)	0.349 (0.065)	0.330 (0.045)
$p_2$	0.2	0.250 (0.066)	0.248 (0.061)	0.245 (0.058)	0.230 (0.033)
$p_3$	0.3	0.358 (0.082)	0.355 (0.076)	0.351 (0.072)	0.331 (0.047)
$p_4$	0.2	0.248 (0.064)	0.246 (0.059)	0.243 (0.056)	0.228 (0.034)
$p_5$	0.3	0.352 (0.084)	0.349 (0.078)	0.345 (0.074)	0.325 (0.045)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		41.59	38.94	36.23	18.02

cases. We explain the unexpected results by noting that the estimation methods based on  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$  do not use optimal weights in  $\mathbf{C}$ , and do not incorporate the additional information on  $\alpha$  in the most efficient way.

### 3.4.3 Simulation 2: Application of Multiple Identification to NE1<sub>b</sub>

In simulation 2, we considered the application of multiple identification to augment the capture history data, assuming the behavioral response model (Model NE1<sub>b</sub>) holds. We used the data generated for the simulation study in Section 3.3 for the standard capture-recapture component of the study ( $x_\gamma$ ). Thus, we have the same three specific cases here.

Case A:  $p = 0.8$  and  $c = 0.5$

Case B:  $p = 0.3$  and  $c = 0.1$

Case C:  $p = 0.3$  and  $c = 0.5$

The same procedure described in Simulation 1 was performed to generate data for the multiple identification component of the study ( $x^*$ ). We randomly chose  $n^*$  histories from the recaptures at the last sampling occasion, and each of them was assigned either correct identification with probability  $\alpha$  or incorrect identification with probability  $(1 - \alpha)$ . Then the number of recaptures that had correct identification was counted. For each data set, the values of  $n^* = 20$  and 40 and known  $\alpha$  were considered.

We considered estimation based on the methods of unweighted least squares and minimum  $\chi^2$  that use the quadratic distance functions of  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$ , respectively. However, we considered only the conditional (on  $x_{all}$ ) approach here. The performance of the estimators was again assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  based on 100 simulated data sets, and the model here is denoted as **Model NE1<sub>b,α</sub>**. When the estimation process failed to converge, those estimates were excluded from the computation of the results. The results for cases A to C are summarized in Tables 3.15 - 3.17. Note that  $n^* = 0$  indicates that the study that did not include additional information from multiple identification. Thus, the results for  $n^* = 0$  are exactly the same as those presented in Tables 3.8 - 3.10, but they are presented here for comparison purposes.

Table 3.15: [Simulation 2: case A] Application of multiple identification to  $NE1_b$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{b,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	1000	998 (32)	998 (32)	998 (32)	997 (33)
$\alpha$	0.7	0.701 (0.012)	0.700 (0.012)	0.700 (0.012)	--
$p$	0.8	0.804 (0.037)	0.804 (0.037)	0.804 (0.036)	0.804 (0.033)
$c$	0.5	0.502 (0.023)	0.502 (0.023)	0.502 (0.023)	0.502 (0.022)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.06	32.06	32.06	33.13
$N$	1000	996 (20)	996 (20)	996 (19)	1000 (21)
$\alpha$	0.8	0.799 (0.010)	0.799 (0.010)	0.799 (0.010)	--
$p$	0.8	0.804 (0.026)	0.804 (0.026)	0.804 (0.026)	0.801 (0.023)
$c$	0.5	0.504 (0.014)	0.504 (0.014)	0.504 (0.014)	0.502 (0.016)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		20.39	20.39	19.41	21.00
$N$	1000	1001 (17)	1001 (17)	1001 (17)	998 (15)
$\alpha$	0.9	0.901 (0.008)	0.901 (0.008)	0.901 (0.008)	--
$p$	0.8	0.798 (0.022)	0.798 (0.022)	0.798 (0.022)	0.799 (0.019)
$c$	0.5	0.500 (0.012)	0.500 (0.012)	0.500 (0.012)	0.501 (0.012)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		17.02	17.02	17.02	15.13
$N$	200	205 (15)	205 (15)	205 (14)	203 (14)
$\alpha$	0.7	0.704 (0.030)	0.703 (0.029)	0.703 (0.027)	--
$p$	0.8	0.782 (0.080)	0.782 (0.079)	0.783 (0.078)	0.784 (0.072)
$c$	0.5	0.486 (0.050)	0.487 (0.049)	0.487 (0.048)	0.489 (0.047)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		15.81	15.81	14.86	14.31
$N$	200	203 (11)	203 (11)	203 (10)	200 (10)
$\alpha$	0.8	0.806 (0.027)	0.806 (0.026)	0.806 (0.026)	--
$p$	0.8	0.786 (0.069)	0.786 (0.068)	0.786 (0.067)	0.794 (0.052)
$c$	0.5	0.494 (0.038)	0.494 (0.037)	0.494 (0.037)	0.500 (0.032)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		11.40	11.40	10.44	10.00
$N$	200	201 (7)	201 (7)	201 (6)	201 (7)
$\alpha$	0.9	0.901 (0.017)	0.901 (0.017)	0.901 (0.017)	--
$p$	0.8	0.792 (0.049)	0.792 (0.049)	0.792 (0.048)	0.792 (0.044)
$c$	0.5	0.496 (0.026)	0.496 (0.026)	0.496 (0.025)	0.496 (0.026)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	7.07	6.08	7.07

Table 3.15 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	1000	1005 (24)	1005 (24)	1005 (24)	995 (25)
$\alpha$	0.7	0.704 (0.012)	0.704 (0.012)	0.704 (0.012)	--
$p$	0.8	0.797 (0.023)	0.797 (0.023)	0.797 (0.023)	0.802 (0.020)
$c$	0.5	0.501 (0.016)	0.501 (0.016)	0.501 (0.016)	0.505 (0.014)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		24.51	24.51	24.51	25.49
$N$	1000	1001 (15)	1001 (15)	1001 (15)	998 (18)
$\alpha$	0.8	0.801 (0.009)	0.801 (0.009)	0.801 (0.009)	--
$p$	0.8	0.800 (0.018)	0.800 (0.018)	0.800 (0.018)	0.801 (0.018)
$c$	0.5	0.504 (0.012)	0.504 (0.012)	0.504 (0.012)	0.504 (0.011)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		15.03	15.03	15.03	18.11
$N$	1000	1002 (15)	1001 (14)	1002 (14)	998 (14)
$\alpha$	0.9	0.901 (0.008)	0.901 (0.008)	0.901 (0.008)	--
$p$	0.8	0.798 (0.017)	0.798 (0.017)	0.798 (0.017)	0.799 (0.015)
$c$	0.5	0.500 (0.012)	0.500 (0.012)	0.500 (0.012)	0.501 (0.011)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		15.13	14.03	14.14	14.14
$N$	200	205 (11)	205 (11)	204 (11)	198 (10)
$\alpha$	0.7	0.714 (0.028)	0.714 (0.027)	0.714 (0.027)	--
$p$	0.8	0.788 (0.058)	0.789 (0.057)	0.789 (0.057)	0.805 (0.049)
$c$	0.5	0.503 (0.034)	0.503 (0.033)	0.504 (0.033)	0.516 (0.028)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		12.08	12.08	11.70	10.19
$N$	200	206 (9)	206 (9)	206 (9)	199 (8)
$\alpha$	0.8	0.815 (0.024)	0.814 (0.024)	0.814 (0.024)	--
$p$	0.8	0.779 (0.051)	0.779 (0.051)	0.779 (0.051)	0.796 (0.042)
$c$	0.5	0.497 (0.032)	0.497 (0.031)	0.497 (0.031)	0.509 (0.027)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		10.81	10.81	10.81	8.06
$N$	200	203 (6)	203 (6)	203 (6)	200 (6)
$\alpha$	0.9	0.905 (0.015)	0.905 (0.015)	0.905 (0.015)	--
$p$	0.8	0.778 (0.041)	0.778 (0.041)	0.779 (0.041)	0.784 (0.038)
$c$	0.5	0.497 (0.025)	0.497 (0.025)	0.497 (0.025)	0.501 (0.023)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		6.70	6.70	6.70	6.00

Table 3.16: [Simulation 2: case B] Application of multiple identification to NE1<sub>b</sub>. Average estimates (with standard errors in parentheses) under the Model NE1<sub>b,α</sub>. Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	1000	1031 (264)	1006 (234)	982 (185)	1003 (48)
$\alpha$	0.7	0.765 (0.208)	0.734 (0.176)	0.701 (0.122)	--
$p$	0.3	0.318 (0.101)	0.322 (0.094)	0.323 (0.082)	0.302 (0.023)
$c$	0.1	0.109 (0.071)	0.112 (0.067)	0.114 (0.057)	0.099 (0.010)
non-conv.		0	1	2	0
$\sqrt{\text{MSE}(\hat{N})}$		265.81	234.07	185.87	48.09
$N$	1000	957 (226)	950 (210)	949 (174)	998 (41)
$\alpha$	0.8	0.789 (0.176)	0.779 (0.160)	0.771 (0.126)	--
$p$	0.3	0.340 (0.102)	0.340 (0.098)	0.335 (0.087)	0.302 (0.023)
$c$	0.1	0.125 (0.066)	0.125 (0.062)	0.121 (0.053)	0.100 (0.008)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		230.05	215.87	181.32	41.04
$N$	1000	928 (178)	934 (171)	952 (153)	1001 (39)
$\alpha$	0.9	0.849 (0.140)	0.853 (0.132)	0.866 (0.117)	--
$p$	0.3	0.343 (0.089)	0.340 (0.086)	0.330 (0.078)	0.301 (0.021)
$c$	0.1	0.130 (0.058)	0.127 (0.056)	0.121 (0.050)	0.101 (0.008)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		192.01	183.29	160.35	39.01
$N$	200	213 (66)	199 (42)	200 (31)	201 (22)
$\alpha$	0.7	0.804 (0.223)	0.703 (0.112)	0.700 (0.071)	--
$p$	0.3	0.329 (0.159)	0.327 (0.121)	0.312 (0.078)	0.304 (0.050)
$c$	0.1	0.114 (0.107)	0.114 (0.072)	0.105 (0.047)	0.100 (0.026)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		67.26	42.01	31.00	22.02
$N$	200	190 (66)	195 (42)	203 (29)	206 (21)
$\alpha$	0.8	0.771 (0.223)	0.769 (0.120)	0.794 (0.067)	--
$p$	0.3	0.372 (0.171)	0.334 (0.127)	0.302 (0.077)	0.292 (0.050)
$c$	0.1	0.150 (0.110)	0.124 (0.076)	0.104 (0.039)	0.098 (0.018)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		66.75	42.29	29.15	21.84
$N$	200	191 (50)	198 (32)	204 (18)	205 (16)
$\alpha$	0.9	0.863 (0.180)	0.876 (0.105)	0.899 (0.051)	--
$p$	0.3	0.352 (0.149)	0.319 (0.109)	0.295 (0.044)	0.293 (0.042)
$c$	0.1	0.137 (0.092)	0.115 (0.056)	0.101 (0.022)	0.099 (0.018)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		50.80	32.06	18.43	16.76

Table 3.16 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	1000	868 (153)	885 (125)	901 (113)	969 (45)
$\alpha$	0.7	0.638 (0.109)	0.646 (0.082)	0.655 (0.070)	--
$p$	0.3	0.364 (0.067)	0.353 (0.056)	0.345 (0.051)	0.315 (0.023)
$c$	0.1	0.147 (0.048)	0.139 (0.040)	0.134 (0.034)	0.113 (0.011)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		202.07	169.85	150.23	54.64
$N$	1000	858 (144)	877 (116)	896 (104)	976 (38)
$\alpha$	0.8	0.713 (0.108)	0.725 (0.085)	0.738 (0.071)	--
$p$	0.3	0.367 (0.063)	0.355 (0.052)	0.345 (0.046)	0.311 (0.021)
$c$	0.1	0.148 (0.043)	0.140 (0.034)	0.134 (0.030)	0.111 (0.009)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		202.23	169.07	147.07	44.94
$N$	1000	889 (128)	905 (113)	918 (99)	989 (35)
$\alpha$	0.9	0.820 (0.103)	0.832 (0.090)	0.842 (0.078)	--
$p$	0.3	0.350 (0.056)	0.342 (0.050)	0.335 (0.043)	0.306 (0.019)
$c$	0.1	0.140 (0.039)	0.135 (0.034)	0.130 (0.029)	0.110 (0.009)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		169.42	147.62	128.54	36.68
$N$	200	167 (53)	169 (37)	172 (31)	180 (18)
$\alpha$	0.7	0.677 (0.178)	0.668 (0.096)	0.675 (0.072)	--
$p$	0.3	0.412 (0.136)	0.388 (0.103)	0.375 (0.087)	0.349 (0.052)
$c$	0.1	0.189 (0.104)	0.172 (0.075)	0.163 (0.063)	0.144 (0.034)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		62.43	48.27	41.77	26.90
$N$	200	166 (49)	175 (33)	180 (26)	192 (17)
$\alpha$	0.8	0.727 (0.167)	0.748 (0.101)	0.762 (0.069)	--
$p$	0.3	0.401 (0.133)	0.361 (0.091)	0.344 (0.070)	0.316 (0.048)
$c$	0.1	0.191 (0.101)	0.163 (0.068)	0.151 (0.051)	0.132 (0.025)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		59.64	41.40	32.80	18.78
$N$	200	170 (40)	179 (30)	184 (26)	197 (14)
$\alpha$	0.9	0.805 (0.138)	0.835 (0.095)	0.856 (0.080)	--
$p$	0.3	0.383 (0.113)	0.354 (0.085)	0.340 (0.072)	0.311 (0.038)
$c$	0.1	0.177 (0.084)	0.157 (0.064)	0.147 (0.055)	0.127 (0.023)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		50.00	36.61	30.52	14.31

Table 3.17: [Simulation 2: case C] Application of multiple identification to  $NE1_b$ . Average estimates (with standard errors in parentheses) under the Model  $NE1_{b,\alpha}$ . Estimates are based on 100 simulated data sets, and  $n^*$  indicates the sample size used for multiple identification.

$n^*$		least squares			
		0	20	40	known $\alpha$
$N$	1000	1005 (148)	1004 (146)	1004 (145)	1007 (67)
$\alpha$	0.7	0.698 (0.028)	0.698 (0.027)	0.698 (0.027)	--
$p$	0.3	0.306 (0.049)	0.306 (0.048)	0.306 (0.048)	0.301 (0.029)
$c$	0.5	0.506 (0.051)	0.507 (0.051)	0.507 (0.050)	0.499 (0.026)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		148.08	146.05	145.05	67.36
$N$	1000	1005 (93)	1005 (92)	1005 (92)	1009 (55)
$\alpha$	0.8	0.799 (0.018)	0.799 (0.018)	0.799 (0.018)	--
$p$	0.3	0.302 (0.035)	0.302 (0.035)	0.302 (0.035)	0.299 (0.026)
$c$	0.5	0.501 (0.030)	0.501 (0.030)	0.501 (0.030)	0.497 (0.020)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		93.13	92.13	92.13	55.73
$N$	1000	1021 (70)	1021 (69)	1021 (69)	1009 (45)
$\alpha$	0.9	0.902 (0.015)	0.902 (0.015)	0.902 (0.015)	--
$p$	0.3	0.294 (0.029)	0.294 (0.029)	0.294 (0.029)	0.297 (0.023)
$c$	0.5	0.496 (0.019)	0.496 (0.019)	0.496 (0.019)	0.499 (0.018)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		73.08	72.12	72.12	45.89
$N$	200	241 (137)	220 (80)	220 (83)	211 (42)
$\alpha$	0.7	0.710 (0.072)	0.702 (0.056)	0.702 (0.047)	--
$p$	0.8	0.299 (0.112)	0.304 (0.099)	0.302 (0.094)	0.297 (0.072)
$c$	0.5	0.502 (0.123)	0.508 (0.105)	0.504 (0.093)	0.496 (0.062)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		143.00	82.46	85.37	43.41
$N$	200	213 (50)	210 (45)	208 (40)	204 (27)
$\alpha$	0.8	0.807 (0.042)	0.805 (0.037)	0.804 (0.035)	--
$p$	0.3	0.295 (0.071)	0.297 (0.067)	0.297 (0.063)	0.299 (0.056)
$c$	0.5	0.503 (0.067)	0.506 (0.061)	0.506 (0.060)	0.507 (0.041)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		51.66	46.09	40.79	27.29
$N$	200	203 (32)	202 (30)	203 (31)	202 (23)
$\alpha$	0.9	0.900 (0.037)	0.899 (0.034)	0.900 (0.032)	--
$p$	0.3	0.310 (0.063)	0.311 (0.061)	0.309 (0.060)	0.307 (0.055)
$c$	0.5	0.495 (0.055)	0.497 (0.052)	0.495 (0.051)	0.491 (0.036)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.14	30.06	31.14	23.08

Table 3.17 (continued.)

$n^*$		minimum $\chi^2$			
		0	20	40	known $\alpha$
$N$	1000	998 (99)	998 (98)	997 (97)	981 (51)
$\alpha$	0.7	0.703 (0.022)	0.703 (0.022)	0.703 (0.021)	--
$p$	0.3	0.308 (0.036)	0.308 (0.036)	0.308 (0.035)	0.311 (0.025)
$c$	0.5	0.505 (0.035)	0.505 (0.035)	0.505 (0.034)	0.508 (0.019)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		99.02	98.02	97.04	54.42
$N$	1000	1003 (70)	1003 (71)	1003 (70)	994 (48)
$\alpha$	0.8	0.802 (0.016)	0.802 (0.016)	0.802 (0.016)	--
$p$	0.3	0.303 (0.028)	0.303 (0.028)	0.303 (0.027)	0.305 (0.022)
$c$	0.5	0.502 (0.025)	0.502 (0.025)	0.502 (0.025)	0.504 (0.016)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		70.06	71.06	70.06	48.37
$N$	1000	1015 (58)	1014 (58)	1015 (58)	1000 (36)
$\alpha$	0.9	0.904 (0.015)	0.904 (0.015)	0.904 (0.015)	--
$p$	0.3	0.298 (0.023)	0.298 (0.023)	0.298 (0.023)	0.301 (0.018)
$c$	0.5	0.497 (0.019)	0.497 (0.019)	0.497 (0.019)	0.501 (0.014)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		59.90	59.66	59.90	36.00
$N$	200	204 (51)	203 (47)	201 (43)	185 (20)
$\alpha$	0.7	0.721 (0.050)	0.720 (0.047)	0.718 (0.044)	--
$p$	0.3	0.326 (0.075)	0.328 (0.073)	0.328 (0.071)	0.346 (0.055)
$c$	0.5	0.516 (0.077)	0.517 (0.073)	0.518 (0.070)	0.537 (0.042)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		51.15	47.09	43.01	25.00
$N$	200	205 (32)	205 (30)	204 (30)	191 (19)
$\alpha$	0.8	0.819 (0.037)	0.818 (0.035)	0.817 (0.035)	--
$p$	0.3	0.309 (0.060)	0.310 (0.058)	0.310 (0.058)	0.327 (0.048)
$c$	0.5	0.509 (0.057)	0.510 (0.055)	0.511 (0.055)	0.527 (0.033)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.38	30.41	30.26	21.02
$N$	200	200 (25)	200 (24)	200 (24)	194 (16)
$\alpha$	0.9	0.908 (0.032)	0.908 (0.031)	0.908 (0.031)	--
$p$	0.3	0.322 (0.053)	0.322 (0.053)	0.322 (0.052)	0.328 (0.044)
$c$	0.5	0.498 (0.047)	0.498 (0.046)	0.498 (0.046)	0.504 (0.030)
non-conv.		0	0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		25.00	24.00	24.00	17.08

For case A, it is clear from the simulation results that the estimates of  $N$  were not improved by performing the multiple identification when population size was large. When the population size was small, no improvement was noted in most cases. However, for some cases, a slight improvement in precision, bias or both was evident when multiple identification was performed. For case B, the precision in  $\hat{N}$  was improved by performing the multiple identification, and the improvement was greater for the cases with  $n^* = 40$  than with  $n^* = 20$ . Also, in some cases, a decrease in bias in  $\hat{N}$  was evident. For case C, there were no obvious improvement in  $\hat{N}$  by performing multiple identification when population size was large. When population size was small, we noted greater improvement in  $\hat{N}$ , especially for the cases with high misidentification rate, compared to the cases with a large population size.

### 3.5 Discussion

In Chapter 1, we discussed the difficulty of applying likelihood theory to the full data set when misidentification is possible. The conditional likelihood approach demonstrated in this chapter is a compromise in which we can develop a statistical model and estimators based on likelihood theory. However, only part of data can be used. Given that the probability of recapture is high, a relatively small fraction of real histories is omitted by conditioning on two or more captures, and there is little loss of information. However, when capture probabilities (and hence the chance of recapture) are low, a larger fraction of the data is omitted in the conditional likelihood, resulting in negative effects on the estimates, especially their precision. It is clear that, for some cases, there is some additional information that cannot be obtained by likelihood-based approach, which uses only part of the data. However, the conditional likelihood approach may have advantages as long as the purpose of the study is estimation of population size and the study has high capture probabilities. One advantage is that assumption of constant correct identification rate may be relaxed because we are estimating the product of capture probability and correct identification rate. Also,  $\mathcal{L}_c$  is multinomial and thus programs such as SURVIV can be used to obtain conditional likelihood estimates and standard errors for  $P'_i$  for a real data set. Then the covariance matrix of the  $\hat{P}'_i$  can be output and used to estimate variance of  $\hat{N}_c$  by using the delta method.

The cases with behavioral response in capture probabilities also showed overestimation of population size when misidentification was ignored, similar to using the  $M_t$  estimator when there

is misidentification as well as temporal variation in capture probabilities. In addition, such positive bias is larger when positive behavioral response is present. We suspected that it may be difficult to estimate both behavioral response and misidentification, particularly negative behavioral response, because both mechanisms affect the probability of recapture. However, estimators under Model NE1<sub>b</sub> seem to have reasonable performance when capture probabilities are high. On the other hand, when capture probabilities are low, the model seemed to have difficulty in separating the behavioral response and misidentification, particularly the negative behavioral response. In general, there seemed to be a trend that estimates of population size under Model NE1<sub>b</sub> are negatively biased when negative behavioral response is present, and positively biased when positive behavioral response is present. Also,  $\hat{N}$  under Model NE1<sub>b</sub> with negative behavioral response were more biased and less precise whereas those with positive behavioral response were less biased and more precise compared to  $\hat{N}$  under Model NE1<sub>t</sub> we examined in Chapter 2.

Improvements in the estimates were evident for most of the low capture probability cases by augmenting capture histories with extra information on misidentification rate, whereas improvements were not evident for high capture probability cases. For the high capture probability cases, the sample size used for multiple identification (i.e.,  $n^* = 20$  or  $40$ ) is small compared to the number of capture histories observed (e.g., the expected number of capture histories observed for case 1 with  $\alpha = 0.7$  in Simulation 1 is approximately 2000). Also, the standard error of  $\hat{\alpha}$  without multiple identification was small compared to that from multiple identification (e.g., for case 1 with  $\alpha = 0.7$  in Simulation 1, the standard error of  $\hat{\alpha}$  without multiple identification is approximately 0.01 compared to the binominal standard error of  $\hat{\alpha}$  for  $n^* = 20$  or  $40$  being approximately 0.1). Thus, for the high capture probability cases that we studied, the extra data included does not make much difference in the performance of the estimator. On the other hand, for the low capture probability cases, the sample size used in the multiple identification component is large relative to the number of capture histories observed, and the standard error of  $\hat{\alpha}$  without multiple identification was large compared to that from multiple identification. Thus, the extra data included does provide additional information to improve the performance of the estimator, and augmentation by including extra data on misidentification rate seems to have a clear advantage for these cases.

Another reason for the unexpected trends in the estimates for high capture probability cases when multiple identification was performed is that the methods of unweighted least squares and minimum  $\chi^2$  are not the most efficient methods, and it is not clear whether we are using the

most efficient weights in the quadratic distance function when the extra information is added. Consequently, we may not observe the properties that we would expect if we were using a fully efficient method such as maximum likelihood. The weights are particularly important for high capture probability cases because the information in the data from capture-recapture component is already high, and using less than optimal weights when the data from capture-recapture are augmented with the data from multiple identification could lead to the unexpected trends observed in the results. On the other hand, for low capture probability cases, augmenting with data from the multiple identification component without optimal weights still improves the estimates because information in the data from the capture-recapture component is not high. Thus, the most likely reason for the unexpected trends we observed is that our method of estimation is a type of quasi-likelihood, not a standard likelihood method. An alternative approach for analyses of augmented data is to use the conditional likelihood approach described in Section 3.2 for the data from capture-recapture component and treat the data from multiple identification as binomial. In this way, a likelihood-based function can be constructed for the augmented data. In future research, the benefit of supplemental data needs to be investigated further over a range of scenarios that reflect a wide range of population sizes, capture probabilities and correct identification rates. Also, possible differences between estimation methods and the effect of sample size for data augmentation are also important future topics.

One aspect that needs to be mentioned about multiple identification is that multiple identification based on the samples only provides information on errors that are related to processing samples in the laboratory. There are other possible causes of misidentification (such as contamination of samples in the field), and the true value of  $\alpha$  may be lower than the estimate of  $\alpha$  from multiple identification.

We here considered the genetic tag-based capture-recapture study, however, the idea of multiple identification can be applied to photographic tag-based capture-recapture studies. For example, researchers can take multiple photographs of natural marks, and then obtain extra information on the misidentification rate by matching the multiple photographs independently. We also only discussed augmentation of data in terms of multiple identification with a simple study design. However, there are different study designs that can be applied to obtain extra information on the misidentification rate. For example, multiple identification can be performed at every sampling occasion. Such data can be used as extra information on the misidentification rate as we demon-

strated in this chapter, but they also provide information that can be used to test for a constant misidentification rate across sampling occasions. Also, there are different ways of augmenting data. For example, we can mark a subset of captured animals by applied tags instead of multiple identification, and then more accurate information on misidentification rates can be obtained. Or, some capture-recapture studies use both genetic and photographic tags (e.g., Anderson et al., 2001; Stevick et al., 2001), and such studies can treat genetic tags as a second type of tag (or as more conventional tags) because identification based on genetic tags can be very accurate if high quality DNA analyses are performed. However, high quality DNA analyses can be very expensive, and understanding the benefit of augmentation of data, such as the amount of improvement in the estimates in relation to the number of additional tags needed, will be valuable information to design studies effectively.

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## Chapter 4

# Photographic Tag-based Capture-Recapture Studies: Models NE2 and EV

### 4.1 Introduction

Photographic identification is one commonly used technique to obtain capture-recapture data. This technique typically uses visible features of an animal, and individual animals are identified at capture and recapture based on comparison with photographic records of these natural marks (*photographic tags*). There are many features that can be used as photographic tags; patterns of wear and damage to the leafy appendages for leafy seadragons (Connolly et al., 2002); spot patterns for cheetahs (Kelly, 2001); blotch structure and arrangement for pythons (Bhupathy, 1991; Vijayakumar, 1999); head marking for adders (Sheldon and Bradley, 1989); facial marking for snow leopards (Blomqvist and Nystrom, 1980); tail marks for crocodiles (Swanepoel, 1996); pigmentation variation for anemonefish (Nelson et al., 1994); stripe patterns for tigers (Karanth et al., 2004b); injury scars on manatees (Langtimm et al., 2004); profiles of dorsal fins for bottlenose dolphins (Mazzoil et al., 2004); and body coloration patterns of tiger salamanders (Church et al., 2007). Photographic tags are particularly useful when the animals are difficult to capture physically, and the method has been widely used to study marine mammals. This method is also applied in the study of rare and elusive terrestrial species such as tigers, where the photographic procedures are often automated by setting camera traps (e.g. Karanth, 1995). In this chapter, we consider

the misidentification issue in photographic tag-based capture-recapture studies, focusing on closed populations.

Misidentification can be introduced into photographic tag-based capture-recapture data when photographed natural marks from the same individual cannot be matched. There are mainly two types of errors that cause such failures. The first type of error is related to the quality of photographs. If a photograph fails to capture identifying marks, for example, because the animal was photographed from a bad angle, it may not be possible to match this photograph to others from the same animal. This type of error has the same or a similar misidentification mechanism to that for non-evolving natural tags 1 we discussed in Chapter 2. The other type of error is related to changes in natural marks. When natural marks are modified or disappear over time, the original natural marks do not exist any more. Thus, photographs from the same animal cannot be matched. In a sense, this case is equivalent to the tag loss problem for applied tags.

In general, both of these two types of errors are present in photographic tag-based capture-recapture studies. However, the misidentification due to the second type of errors (i.e., change in natural marks) can be eliminated by choosing the types of natural marks used. For example, it is reasonable to assume that there is no risk of misidentification due to the second type of error when rather permanent natural marks, such as stripe patterns on tigers, are used. In such cases, we only need to consider the risk of misidentification due to the first type of error. On the other hand, some dolphin species are studied by taking photographs of unique profiles of dorsal fins such as scars and nicks. These natural marks have a risk of modification or loss, for example, when dolphins acquire new injuries. Thus, this type of capture-recapture data has a risk of misidentification due to both types of errors. In Chapter 1, we defined two different types of natural tags: those based on natural marks that are not likely to change over time (e.g., coloration patterns), which we refer to as *non-evolving natural tags*, and those based on natural marks that can change over time (e.g., injury scars), which we refer to as *evolving natural tags*. We make this division because the misidentification mechanism in photographic tag-based capture-recapture studies is slightly different between these two types of natural tags. In other words, a photographic tag-based capture-recapture study that uses non-evolving natural tags needs to consider misidentification due to only the first type of error, whereas one that uses evolving natural tags needs to consider misidentification due to both types of error. In the following sections, we first consider the misidentification issue in photographic tag-based capture-recapture studies that

use non-evolving natural tags, and then evolving natural tags.

## 4.2 Non-Evolving Natural Tags 2: Misidentification is Possible Only at Recaptures

### 4.2.1 Proposed Misidentification Mechanism

There are many reasons why the quality of a photograph may be poor. For example, the animal may be moving when photographs are taken, the natural marks may be photographed from a bad angle, or weather conditions may be bad. As a result, it may be difficult to identify the natural marks, and misidentification is likely. It is often the case that poor quality photographs are discarded, and not used to obtain capture history data. However, it is beneficial to have models that allow for errors in capture-recapture data so that marginal quality photographs can be included, and we here assume that the data always have a risk of containing errors due to misidentification that is related to quality of photographs. Although misidentification mechanism NE1 considered in Chapter 2 can be applied to this type of misidentification, we here consider a variation of NE1 and make the following assumptions:

1. Misidentification of animals always leads to false identification of animals that do not exist in the population;
2. The same error is never repeated; and
3. Misidentification can occur only at recapture events.

The basic ideas of this misidentification mechanism are similar to those for non-evolving natural tags 1 that we considered in Chapter 2, and assumptions 1 and 2 are exactly same. For photographic tag-based studies, assumption 1 may be an oversimplified scenario, and it may be more realistic to include the possibility of assigning false identification of existing animals in the population. However, it is a necessary assumption at this point, and we continue our model formulation with assumption 1. Assumption 3 is different because we assume that an animal has been captured with good quality photographs, and thus "tagged" correctly. Then, we consider errors that lead to misidentification of this animal on recapture that are caused by an inability to match subsequent

photographs to the ones on record. Consequently, we assume there is no risk of misidentification for animals at their first capture in this type of misidentification mechanism.

These assumptions together lead to a simple misidentification mechanism with the following characteristics:

- Misidentification can occur at any recapture events;
- If a recaptured animal is incorrectly identified, the recapture event of that animal appears as a non-capture (i.e., the "real" capture history is recorded as [0]), but it also creates a capture history of a non-existing animal (i.e., a "ghost" capture history is created by recording a capture [1] for a fictitious animal for this sampling occasion); and
- Recaptures can occur in a "real" capture history whereas each ghost capture history contains exactly one capture.

This type of misidentification is a variation of non-evolving natural tags 1 and referred to as *non-evolving natural tags 2 (NE2)*. The only difference between NE1 considered in Chapter 2 and NE2 is whether misidentification is possible at the first capture event (NE1) or not (NE2). Whether to use NE1 or NE2 in a particular photographic tag-based capture-recapture study needs to be determined by the researchers. For example, some studies have strict criteria for obtaining good photographic information of animals' visible features before they can be used in capture-recapture studies. In such cases, NE2 seems to be the more appropriate misidentification mechanism. On the other hand, if a study is not designed to obtain prior photographic information of animals' visible features before they can be used as a part of capture-recapture study, then NE1 seems to be the more appropriate misidentification mechanism.

### 4.2.2 Statistical Model Development

As in Chapter 2, we assume the population is closed during the period of study, and here we use a 3-sample study for illustrative purposes. Terms and notation used here follow those given in the previous chapters (see Tables 1.1 and 2.1). We have a parameter for capture probability of an animal at each sampling occasion,  $p_1$ ,  $p_2$  and  $p_3$ . Also for simplicity, we assume that the probability of correct identification is constant for all animals throughout the study, and we have a parameter for a probability of correct identification for an animal at recapture,  $\alpha$ . Consider

an animal which is captured at all sampling occasions. The animal has true capture history [111], but there are several possibilities for the observable capture histories depending on whether misidentification occurs. One of the possibilities is the pair [101 ; 010], which is the case that misidentification occurred only at the second sampling occasion. Given that an animal has true capture history [111], the probability of observing the animal with real capture history [101] is  $p_1 p_2 (1 - \alpha) p_3 \alpha$ . Misidentification at sample 2 also creates a ghost capture history [010], which has the same probability  $p_1 p_2 (1 - \alpha) p_3 \alpha$ , because of the complete dependency of this pair of real and ghost capture histories. Table 4.1 presents the probability of all the observable capture histories conditioned on the true capture history for the 3-sample case. The marginal probabilities for the observed capture histories in the 3-sample case are summarized in Table 4.2 where  $P'_i = p_i \alpha$  and  $Q'_i = (1 - P'_i)$ . Notice that the total probability exceeds 1 because of the ghost capture histories created, as was the case for non-evolving natural tags 1, and it equals 1 if and only if no misidentification occurs (i.e.,  $\alpha = 1$ ).

Let  $t_1(\gamma)$  be the sampling occasion when the first capture occurs for a given capture history  $\gamma$ . Then the general expression for the probability of observing capture history  $\gamma$  for the  $K$ -sample case is

$$\Pr[\gamma] = \left[ \prod_{i=1}^{t_1(\gamma)} p_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} \right] \left[ \prod_{i=t_1(\gamma)+1}^K P_i^{\gamma_i} (1 - P_i)^{(1-\gamma_i)} \right]$$

for  $\gamma$  with multiple capture events or with a single capture event and  $t_1(\gamma) = 1$ , and

$$\Pr[\gamma] = \left[ \prod_{i=1}^{t_1(\gamma)} p_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} \right] \left[ \prod_{i=t_1(\gamma)+1}^K P_i^{\gamma_i} (1 - P_i)^{(1-\gamma_i)} \right] + \sum_{i=1}^{t_1(\gamma)-1} \left[ \prod_{j=0}^{i-1} (1 - p_j) p_i \right] p_{t_1(\gamma)} (1 - \alpha)$$

for  $\gamma$  with a single capture event and  $t_1(\gamma) > 1$  where

- $\gamma_i$  is the  $i$ th entry of capture history  $\gamma$
- $p_i$  is the capture probability of an animal at the  $i$ th sampling occasion;  $p_j = 0$  if  $j = 0$
- $\alpha$  is the probability of correct identification
- $P'_i = p_i \alpha$
- $Q'_i = (1 - P'_i)$ .

Table 4.1: A summary of the observable capture histories and associated probabilities for non-evolving natural tags 2 for the 3-sample case.

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma \mid \omega]$	
111	none	111	real	$p_1 p_2 \alpha p_3 \alpha$	
		at third	110	real	$p_1 p_2 \alpha p_3 (1 - \alpha)$
			001	ghost*	$p_1 p_2 \alpha p_3 (1 - \alpha)$
	at second	101	real	$p_1 p_2 (1 - \alpha) p_3 \alpha$	
		010	ghost*	$p_1 p_2 (1 - \alpha) p_3 \alpha$	
	at second and third	100	real	$p_1 p_2 (1 - \alpha) p_3 (1 - \alpha)$	
		010	ghost*	$p_1 p_2 (1 - \alpha) p_3 (1 - \alpha)$	
		001	ghost*	$p_1 p_2 (1 - \alpha) p_3 (1 - \alpha)$	
	110	none	110	real	$p_1 p_2 \alpha (1 - p_3)$
100			real	$p_1 p_2 (1 - \alpha) (1 - p_3)$	
at second		010	ghost*	$p_1 p_2 (1 - \alpha) (1 - p_3)$	
101	none	101	real	$p_1 (1 - p_2) p_3 \alpha$	
		100	real	$p_1 (1 - p_2) p_3 (1 - \alpha)$	
	at third	001	ghost*	$p_1 (1 - p_2) p_3 (1 - \alpha)$	
100	none	100	real	$p_1 (1 - p_2) (1 - p_3)$	
011	none	011	real	$(1 - p_1) p_2 p_3 \alpha$	
		third	010	real	$(1 - p_1) p_2 p_3 (1 - \alpha)$
	001		ghost*	$(1 - p_1) p_2 p_3 (1 - \alpha)$	
010	none	010	real	$(1 - p_1) p_2 (1 - p_3)$	
001	none	001	real	$(1 - p_1) (1 - p_2) p_3$	
000	none	000	real	$(1 - p_1) (1 - p_2) (1 - p_3)$	

Table 4.2: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for non-evolving natural tags 2 in a 3-sample study.

$\gamma$ (observed history)	Pr[ $\gamma$ ]	
111	$p_1 P'_2 P'_3$	
110	$p_1 P'_2 Q'_3$	
101	$p_1 Q'_2 P'_3$	
100	$p_1 Q'_2 Q'_3$	
011	$q_1 p_2 P'_3$	
010	$q_1 p_2 Q'_3$	+ $p_1 p_2 (1 - \alpha)$
001	$q_1 q_2 p_3$	+ $(q_1 p_2 + p_1) p_3 (1 - \alpha)$
000	$q_1 q_2 q_3$	
Total**	$1 + [p_1 p_2 + q_1 p_2 p_3 + p_1 p_3](1 - \alpha)$	

\*\* Total = 1 if and only if  $\alpha = 1$ .

### 4.2.3 Estimation

As was the case for non-evolving natural tags 1, a multinomial approach to building a likelihood for the observed histories is invalid because of the dependency between pairs of real and ghost histories, and the total probability here exceeds 1. Again we apply the methods of unweighted least squares and minimum  $\chi^2$ , both of which are based on the idea of using the observed values and marginal expected values of  $\mathbf{X}_\gamma$  to obtain estimates. The marginal expected values of  $\mathbf{X}_\gamma$  for

the 3-sample case can be written as

$$\begin{aligned}
E[X_{111}] &= N [p_1 P'_2 P'_3] \\
E[X_{110}] &= N [p_1 P'_2 Q'_3] \\
E[X_{101}] &= N [p_1 Q'_2 P'_3] \\
E[X_{100}] &= N [p_1 Q'_2 Q'_3] \\
E[X_{011}] &= N [q_1 p_2 P'_3] \\
E[X_{010}] &= N [q_1 p_2 Q'_3 + p_1 p_2 (1 - \alpha)] \\
E[X_{001}] &= N [q_1 q_2 p_3 + (q_1 p_2 + p_1) p_3 (1 - \alpha)] \\
E[X_{000}] &= N [q_1 q_2 q_3] ,
\end{aligned}$$

where  $X_{000}$  is not observable. Then, the estimates are obtained by minimizing the quadratic distance functions

$$\mathcal{F}_{ls} = \sum_{\gamma, \gamma \neq 000} (x_\gamma - E[X_\gamma])^2$$

or

$$\mathcal{F}_{\chi^2} = \sum_{\gamma, \gamma \neq 000} \frac{(x_\gamma - E[X_\gamma])^2}{E[X_\gamma]}$$

where  $x_\gamma$  represents the data and  $X_\gamma$  represents the random variable.

Estimators can also be obtained by conditioning on the total number of capture histories observed,  $X_{all}$ . The total probability associated with the observed capture histories is

$$\begin{aligned}
p^* &= 1 - q_1 q_2 q_3 + [p_1 p_2 + q_1 p_2 p_3 + p_1 p_3] (1 - \alpha) \\
&= 1 - q_1 q_2 q_3 + [q_1 q_2 q_3 - 1 + p_1 + p_2 + p_3] (1 - \alpha)
\end{aligned}$$

for the 3-sample case, or in general,

$$p^* = 1 - \prod_{i=1}^K (1 - p_i) + \left[ \prod_{i=1}^K (1 - p_i) - 1 + \sum_{i=1}^K p_i \right] (1 - \alpha)$$

for the  $K$ -sample case. Then the expected values of  $\mathbf{X}_\gamma$  with the conditional approach can be

written as

$$E[X_\gamma | X_{all} = x_{all}] = \frac{x_{all} \Pr[\gamma]}{p^*}$$

where  $x_{all}$  is the total number of capture histories observed. Again, the estimates are obtained by minimizing the quadratic distance function  $\mathcal{F}_{ls}$  or  $\mathcal{F}_{\chi^2}$  as described for the unconditional approach. With the conditional approach, the parameter  $N$  is removed from the estimation process and estimated as a derived parameter,

$$\hat{N} = \frac{x_{all}}{\hat{p}^*}.$$

#### 4.2.4 Simulation Study

##### Simulation 1: Cases with Time Specific Capture Probabilities

In our simulation study, we considered a closed population of  $N$  animals, and the data were generated for a study with  $K = 5$  sampling occasions. We allowed for the capture probability to be time specific, and each animal was subject to capture with probability  $p_i$  at each sampling occasion  $i$ . When an animal was captured for the first time, the animal was not subject to misidentification. However, whenever an animal was recaptured, identification of the animal was either correct with probability  $\alpha$ , or incorrect with probability  $(1 - \alpha)$ . If the identification was correct, the capture event of the animal was recorded as capture (i.e., [1]). However, if the identification was incorrect, the event was recorded as non-capture (i.e., [0]) in the real history, and a ghost history was created in which the event was recorded as a capture (i.e., [1]). Then, each animal was again subject to capture at the next sampling occasion (see Figure 4.1). Note that real capture histories can contain recaptures. However, a ghost capture history cannot contain any recaptures, and misidentification always creates a new ghost capture history with a single capture at the sample when incorrect identification occurs.

Parameter values were chosen to reflect a wide range of population sizes, capture probabilities and correct identification rates. We considered the same four specific cases as we did for non-evolving natural tags 1.

$$\text{Case 1: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 2: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

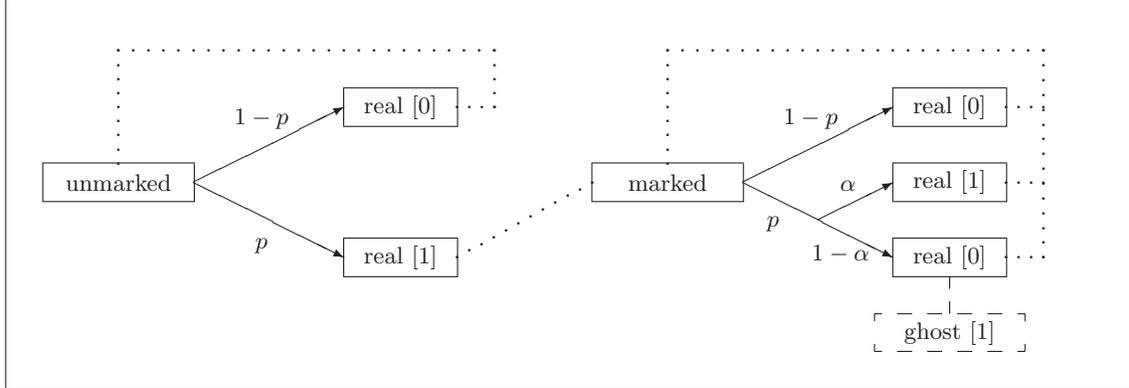


Figure 4.1: A diagram of the misidentification mechanism for non-evolving natural tags 2.

Case 3:  $N = 1000$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

Case 4:  $N = 200$  and  $\mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$

Each combination of parameter values is describing either a large or a small population size with high or low capture probabilities, and for each case, correct identification rates of  $\alpha = 0.7, 0.8,$  and  $0.9$  were considered. We considered estimation methods based on unweighted least squares and minimum  $\chi^2$ , based on the quadratic distance functions  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$ , respectively. In addition, unconditional and conditional (on  $x_{all}$ ) approaches were considered. We were also interested in the comparison of estimates obtained under our NE2 model (**Model NE2<sub>t</sub>**) and the corresponding conventional capture-recapture model (**Model M<sub>t</sub>**). Thus, maximum likelihood estimates (conditional on  $x_{all}$ ) assuming Model M<sub>t</sub> to be correct were also obtained for the same generated data sets.

The performance of the two estimation methods under Model NE2<sub>t</sub> and maximum likelihood under Model M<sub>t</sub> was assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  over 100 simulated data sets. The results for cases 1 to 4 are summarized in Tables 4.3 - 4.6. Although we considered unconditional and conditional (on  $x_{all}$ ) approaches for estimation of  $N$  under Model NE2<sub>t</sub>, the unconditional approach displayed numerical problems such as sensitivity to starting values and non-convergence. Thus, only the results from the conditional (on  $x_{all}$ ) approach are presented in the Tables.

Similar to the case for non-evolving natural tags 1, we observed positive bias in  $\hat{N}$  when

Table 4.3: [Simulation 1: case 1] Non-evolving natural tags 2 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	998 (9)	1004 (11)	2011 (41)
$\alpha$	0.7	0.699 (0.009)	0.702 (0.009)	--
$p_1$	0.7	0.699 (0.018)	0.696 (0.016)	0.347 (0.010)
$p_2$	0.8	0.803 (0.016)	0.798 (0.018)	0.399 (0.010)
$p_3$	0.7	0.697 (0.021)	0.696 (0.017)	0.347 (0.010)
$p_4$	0.8	0.800 (0.021)	0.798 (0.017)	0.398 (0.010)
$p_5$	0.7	0.701 (0.020)	0.700 (0.017)	0.349 (0.010)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		9.21	11.70	1011.83
$N$	1000	1000 (7)	1004 (7)	1614 (28)
$\alpha$	0.8	0.800 (0.008)	0.801 (0.008)	--
$p_1$	0.7	0.698 (0.018)	0.695 (0.016)	0.432 (0.012)
$p_2$	0.8	0.800 (0.015)	0.796 (0.014)	0.496 (0.011)
$p_3$	0.7	0.701 (0.017)	0.698 (0.017)	0.434 (0.011)
$p_4$	0.8	0.800 (0.016)	0.797 (0.016)	0.496 (0.011)
$p_5$	0.7	0.700 (0.017)	0.698 (0.015)	0.434 (0.012)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.00	8.06	614.63
$N$	1000	999 (6)	1001 (6)	1287 (16)
$\alpha$	0.9	0.900 (0.006)	0.900 (0.006)	--
$p_1$	0.7	0.699 (0.017)	0.697 (0.015)	0.543 (0.014)
$p_2$	0.8	0.801 (0.013)	0.798 (0.012)	0.622 (0.012)
$p_3$	0.7	0.698 (0.019)	0.696 (0.016)	0.542 (0.013)
$p_4$	0.8	0.802 (0.014)	0.798 (0.013)	0.623 (0.011)
$p_5$	0.7	0.703 (0.018)	0.701 (0.016)	0.546 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		6.08	6.08	287.44

Table 4.4: [Simulation 1: case 2] Non-evolving natural tags 2 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	200 (4)	205 (5)	401 (17)
$\alpha$	0.7	0.700 (0.022)	0.711 (0.021)	--
$p_1$	0.7	0.697 (0.044)	0.689 (0.032)	0.349 (0.021)
$p_2$	0.8	0.801 (0.040)	0.784 (0.042)	0.400 (0.024)
$p_3$	0.7	0.698 (0.045)	0.687 (0.035)	0.348 (0.021)
$p_4$	0.8	0.792 (0.042)	0.783 (0.039)	0.397 (0.022)
$p_5$	0.7	0.695 (0.047)	0.688 (0.038)	0.348 (0.023)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	7.07	201.71
$N$	200	199 (2)	204 (3)	323 (12)
$\alpha$	0.8	0.799 (0.019)	0.806 (0.018)	--
$p_1$	0.7	0.696 (0.036)	0.689 (0.032)	0.433 (0.024)
$p_2$	0.8	0.794 (0.032)	0.779 (0.033)	0.493 (0.025)
$p_3$	0.7	0.701 (0.045)	0.693 (0.041)	0.435 (0.028)
$p_4$	0.8	0.804 (0.034)	0.782 (0.029)	0.497 (0.025)
$p_5$	0.7	0.700 (0.037)	0.694 (0.036)	0.435 (0.025)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	5.00	123.58
$N$	200	200 (2)	201 (2)	257 (7)
$\alpha$	0.9	0.900 (0.013)	0.901 (0.013)	--
$p_1$	0.7	0.703 (0.037)	0.693 (0.031)	0.544 (0.025)
$p_2$	0.8	0.796 (0.032)	0.783 (0.030)	0.621 (0.028)
$p_3$	0.7	0.696 (0.038)	0.692 (0.035)	0.543 (0.029)
$p_4$	0.8	0.798 (0.038)	0.786 (0.031)	0.621 (0.029)
$p_5$	0.7	0.707 (0.040)	0.696 (0.030)	0.547 (0.029)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.00	2.23	57.42

Table 4.5: [Simulation 1: case 3] Non-evolving natural tags 2 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1086 (191)	1021 (143)	1568 (65)
$\alpha$	0.7	0.743 (0.092)	0.725 (0.073)	--
$p_1$	0.3	0.283 (0.052)	0.301 (0.043)	0.191 (0.013)
$p_2$	0.2	0.189 (0.034)	0.203 (0.029)	0.128 (0.009)
$p_3$	0.3	0.283 (0.047)	0.300 (0.041)	0.191 (0.011)
$p_4$	0.2	0.190 (0.036)	0.205 (0.030)	0.129 (0.009)
$p_5$	0.3	0.289 (0.053)	0.305 (0.042)	0.194 (0.012)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		209.46	144.53	571.70
$N$	1000	1022 (159)	982 (125)	1326 (47)
$\alpha$	0.8	0.814 (0.090)	0.805 (0.075)	--
$p_1$	0.3	0.302 (0.049)	0.314 (0.043)	0.227 (0.012)
$p_2$	0.2	0.201 (0.034)	0.212 (0.030)	0.152 (0.011)
$p_3$	0.3	0.301 (0.051)	0.314 (0.044)	0.227 (0.014)
$p_4$	0.2	0.198 (0.033)	0.211 (0.030)	0.151 (0.012)
$p_5$	0.3	0.302 (0.049)	0.313 (0.041)	0.227 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		160.51	126.28	329.37
$N$	1000	1000 (112)	966 (93)	1150 (34)
$\alpha$	0.9	0.898 (0.071)	0.886 (0.063)	--
$p_1$	0.3	0.306 (0.039)	0.317 (0.034)	0.262 (0.014)
$p_2$	0.2	0.203 (0.027)	0.213 (0.022)	0.174 (0.013)
$p_3$	0.3	0.303 (0.040)	0.315 (0.033)	0.261 (0.014)
$p_4$	0.2	0.204 (0.030)	0.213 (0.024)	0.175 (0.013)
$p_5$	0.3	0.303 (0.040)	0.314 (0.033)	0.260 (0.015)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		112.00	99.02	153.80

Table 4.6: [Simulation 1: case 4] Non-evolving natural tags 2 with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	211 (67)	188 (48)	309 (27)
$\alpha$	0.7	0.740 (0.167)	0.731 (0.130)	--
$p_1$	0.3	0.308 (0.106)	0.341 (0.083)	0.191 (0.026)
$p_2$	0.2	0.215 (0.084)	0.248 (0.067)	0.134 (0.024)
$p_3$	0.3	0.320 (0.109)	0.353 (0.088)	0.198 (0.022)
$p_4$	0.2	0.216 (0.077)	0.243 (0.061)	0.132 (0.022)
$p_5$	0.3	0.321 (0.114)	0.353 (0.094)	0.198 (0.025)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		67.89	49.47	112.29
$N$	200	203 (52)	185 (36)	271 (19)
$\alpha$	0.8	0.794 (0.141)	0.792 (0.112)	--
$p_1$	0.3	0.315 (0.095)	0.344 (0.074)	0.221 (0.027)
$p_2$	0.2	0.214 (0.067)	0.242 (0.054)	0.149 (0.024)
$p_3$	0.3	0.313 (0.099)	0.342 (0.077)	0.220 (0.031)
$p_4$	0.2	0.206 (0.063)	0.240 (0.056)	0.148 (0.022)
$p_5$	0.3	0.312 (0.084)	0.341 (0.068)	0.221 (0.027)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		52.08	39.00	73.49
$N$	200	192 (36)	179 (27)	230 (14)
$\alpha$	0.9	0.870 (0.115)	0.862 (0.093)	--
$p_1$	0.3	0.328 (0.075)	0.353 (0.059)	0.263 (0.032)
$p_2$	0.2	0.212 (0.055)	0.242 (0.046)	0.173 (0.024)
$p_3$	0.3	0.325 (0.076)	0.353 (0.063)	0.263 (0.035)
$p_4$	0.2	0.214 (0.053)	0.245 (0.047)	0.175 (0.026)
$p_5$	0.3	0.320 (0.072)	0.349 (0.060)	0.261 (0.036)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		36.87	34.20	33.10

misidentification was ignored, and the bias can be substantial as the value of  $\alpha$  becomes lower (relative bias  $> 50\%$  for  $\alpha = 0.7$  cases). The performance of the  $NE2_t$  estimators was good, especially for the cases with high capture probability (relative bias  $< 3\%$  and relative standard error  $< 3\%$  for cases 1 and 2). However, some bias in  $\hat{N}$  was noted for the cases of low capture probability (relative bias  $\approx 0 - 11\%$  and relative standard error  $\approx 9 - 34\%$  for cases 3 and 4). It was again difficult to differentiate between the methods of unweighted least squares and minimum  $\chi^2$ . However, the method of minimum  $\chi^2$  seemed to have a tendency that  $\hat{N}$  are negatively biased when capture probabilities are low, especially as the value of  $\alpha$  increases. The magnitudes of bias and precision for non-evolving natural tags 2 cases (relative bias  $< 11\%$  and relative standard error  $< 34\%$ ) were better than those for the non-evolving natural tags 1 cases (relative bias  $< 30\%$  and relative standard error  $\leq 60\%$ ). This is as expected because misidentification does not occur at the first capture event with  $NE2$ , and thus there are fewer occasions that misidentification can occur compared to  $NE1$ . An important result is that ignoring misidentification can lead to overestimation of  $N$  as the case for non-evolving natural tags 1. The larger the rate of misidentification, the larger such positive bias in  $\hat{N}$  becomes, and the magnitude of such bias can be substantial as shown by the results.

### Simulation 2: Cases with Time Specific Capture Probabilities (High $\alpha$ )

We also considered cases with lower misidentification rates as we did for non-evolving natural tags 1. We generated new sets of data for the four cases described in the previous section, but with correct identification rates of  $\alpha = 0.950, 0.975$  and  $1.000$ . The data sets were again analyzed using the two estimation methods under Model  $NE2_t$ , and also maximum likelihood (conditional on  $x_{all}$ ) under Model  $M_t$ . Results for cases 1 to 4 are summarized in Tables 4.7 - 4.10. Once again, the unconditional approach of Model  $NE2_t$  had numerical problems. Thus, we have only included the results from the conditional (on  $x_{all}$ ) approach in the Tables.

As we expected, the performance of the Model  $M_t$  estimator improved as the value of  $\alpha$  increased. However, even when the misidentification rate was as low as  $0.025$ , positive bias in  $\hat{N}$  was evident (relative bias  $> 6\%$  and  $3\%$  for  $\alpha = 0.950$  and  $0.975$ , respectively). For high capture probability cases, the Model  $NE2_t$  estimators performed well (relative bias  $< 1\%$  and relative standard error  $\leq 1\%$  for cases 1 and 2), and performance was better than that of Model  $M_t$  even

Table 4.7: [Simulation 2: case 1] Non-evolving natural tags 2 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1000 (4)	1001 (4)	1139 (11)
$\alpha$	0.950	0.950 (0.005)	0.950 (0.004)	--
$p_1$	0.7	0.697 (0.019)	0.696 (0.015)	0.612 (0.014)
$p_2$	0.8	0.800 (0.016)	0.797 (0.012)	0.702 (0.011)
$p_3$	0.7	0.700 (0.019)	0.698 (0.015)	0.615 (0.014)
$p_4$	0.8	0.801 (0.014)	0.796 (0.013)	0.702 (0.013)
$p_5$	0.7	0.700 (0.017)	0.698 (0.014)	0.614 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	4.12	139.43
$N$	1000	999 (5)	999 (5)	1068 (8)
$\alpha$	0.975	0.975 (0.004)	0.975 (0.004)	--
$p_1$	0.7	0.699 (0.018)	0.697 (0.015)	0.653 (0.015)
$p_2$	0.8	0.801 (0.014)	0.798 (0.012)	0.749 (0.013)
$p_3$	0.7	0.697 (0.020)	0.696 (0.015)	0.653 (0.014)
$p_4$	0.8	0.802 (0.014)	0.799 (0.013)	0.750 (0.013)
$p_5$	0.7	0.703 (0.019)	0.701 (0.015)	0.657 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		5.09	5.09	68.46
$N$	1000	998 (2)	997 (3)	1000 (1)
$\alpha$	1.000	0.999 (0.001)	0.999 (0.001)	--
$p_1$	0.7	0.701 (0.018)	0.698 (0.014)	0.699 (0.014)
$p_2$	0.8	0.801 (0.014)	0.799 (0.012)	0.801 (0.012)
$p_3$	0.7	0.700 (0.016)	0.699 (0.014)	0.699 (0.014)
$p_4$	0.8	0.799 (0.016)	0.797 (0.014)	0.799 (0.013)
$p_5$	0.7	0.701 (0.016)	0.698 (0.013)	0.699 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.82	4.24	1.00

Table 4.8: [Simulation 2: case 2] Non-evolving natural tags 2 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	200 (2)	200 (2)	228 (5)
$\alpha$	0.950	0.950 (0.010)	0.951 (0.010)	--
$p_1$	0.7	0.698 (0.037)	0.691 (0.031)	0.613 (0.029)
$p_2$	0.8	0.794 (0.033)	0.780 (0.027)	0.698 (0.028)
$p_3$	0.7	0.702 (0.046)	0.693 (0.039)	0.616 (0.034)
$p_4$	0.8	0.802 (0.031)	0.787 (0.030)	0.704 (0.028)
$p_5$	0.7	0.704 (0.040)	0.695 (0.031)	0.616 (0.030)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.00	2.00	28.44
$N$	200	200 (2)	199 (2)	214 (3)
$\alpha$	0.975	0.975 (0.009)	0.974 (0.008)	--
$p_1$	0.7	0.703 (0.038)	0.693 (0.031)	0.654 (0.030)
$p_2$	0.8	0.797 (0.031)	0.786 (0.030)	0.747 (0.030)
$p_3$	0.7	0.698 (0.040)	0.692 (0.033)	0.653 (0.031)
$p_4$	0.8	0.798 (0.037)	0.786 (0.030)	0.746 (0.030)
$p_5$	0.7	0.703 (0.042)	0.694 (0.029)	0.658 (0.030)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.00	2.23	14.31
$N$	200	199 (1)	199 (1)	200 (1)
$\alpha$	1.000	0.999 (0.002)	0.998 (0.003)	--
$p_1$	0.7	0.706 (0.043)	0.696 (0.036)	0.703 (0.036)
$p_2$	0.8	0.801 (0.032)	0.788 (0.027)	0.800 (0.028)
$p_3$	0.7	0.697 (0.041)	0.689 (0.031)	0.696 (0.033)
$p_4$	0.8	0.803 (0.034)	0.789 (0.030)	0.801 (0.030)
$p_5$	0.7	0.698 (0.044)	0.691 (0.031)	0.697 (0.033)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		1.41	1.41	1.00

Table 4.9: [Simulation 2: case 3] Non-evolving natural tags 2 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE2_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE2_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	997 (93)	977 (83)	1069 (32)
$\alpha$	0.950	0.947 (0.057)	0.943 (0.054)	--
$p_1$	0.3	0.306 (0.034)	0.312 (0.033)	0.282 (0.015)
$p_2$	0.2	0.204 (0.025)	0.211 (0.023)	0.188 (0.013)
$p_3$	0.3	0.303 (0.036)	0.312 (0.033)	0.281 (0.016)
$p_4$	0.2	0.201 (0.026)	0.210 (0.024)	0.188 (0.014)
$p_5$	0.3	0.302 (0.034)	0.311 (0.030)	0.281 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		93.04	86.12	76.05
$N$	1000	967 (70)	953 (66)	1032 (27)
$\alpha$	0.975	0.953 (0.046)	0.950 (0.047)	--
$p_1$	0.3	0.316 (0.029)	0.320 (0.027)	0.292 (0.015)
$p_2$	0.2	0.208 (0.021)	0.215 (0.019)	0.194 (0.014)
$p_3$	0.3	0.312 (0.032)	0.317 (0.026)	0.290 (0.015)
$p_4$	0.2	0.210 (0.024)	0.215 (0.020)	0.195 (0.014)
$p_5$	0.3	0.311 (0.031)	0.317 (0.028)	0.290 (0.017)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		77.38	81.02	41.86
$N$	1000	966 (56)	949 (56)	999 (22)
$\alpha$	1.000	0.975 (0.038)	0.969 (0.041)	--
$p_1$	0.3	0.316 (0.024)	0.322 (0.023)	0.303 (0.016)
$p_2$	0.2	0.208 (0.019)	0.215 (0.020)	0.200 (0.014)
$p_3$	0.3	0.312 (0.028)	0.318 (0.025)	0.300 (0.017)
$p_4$	0.2	0.205 (0.020)	0.214 (0.018)	0.199 (0.014)
$p_5$	0.3	0.311 (0.029)	0.321 (0.026)	0.302 (0.016)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		65.51	75.74	22.02

Table 4.10: [Simulation 2: case 4] Non-evolving natural tags 2 with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $NE_{2t}$  are from the conditional (on  $x_{all}$ ) approach.

		Model $NE_{2t}$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	188 (30)	181 (25)	216 (13)
$\alpha$	0.950	0.904 (0.104)	0.906 (0.086)	--
$p_1$	0.3	0.328 (0.075)	0.346 (0.066)	0.277 (0.033)
$p_2$	0.2	0.223 (0.055)	0.243 (0.049)	0.187 (0.030)
$p_3$	0.3	0.326 (0.076)	0.345 (0.062)	0.276 (0.037)
$p_4$	0.2	0.214 (0.050)	0.243 (0.053)	0.185 (0.029)
$p_5$	0.3	0.324 (0.064)	0.343 (0.056)	0.276 (0.034)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		32.31	31.40	20.61
$N$	200	186 (26)	176 (21)	207 (10)
$\alpha$	0.975	0.922 (0.084)	0.914 (0.074)	--
$p_1$	0.3	0.336 (0.064)	0.357 (0.050)	0.292 (0.035)
$p_2$	0.2	0.216 (0.048)	0.244 (0.040)	0.192 (0.025)
$p_3$	0.3	0.331 (0.069)	0.355 (0.056)	0.292 (0.039)
$p_4$	0.2	0.218 (0.044)	0.246 (0.042)	0.195 (0.028)
$p_5$	0.3	0.324 (0.063)	0.353 (0.054)	0.289 (0.038)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		29.52	31.89	12.20
$N$	200	187 (25)	178 (19)	201 (11)
$\alpha$	1.000	0.947 (0.078)	0.939 (0.069)	--
$p_1$	0.3	0.340 (0.065)	0.356 (0.056)	0.304 (0.039)
$p_2$	0.2	0.219 (0.053)	0.247 (0.040)	0.203 (0.027)
$p_3$	0.3	0.323 (0.062)	0.348 (0.050)	0.298 (0.036)
$p_4$	0.2	0.219 (0.055)	0.239 (0.046)	0.197 (0.034)
$p_5$	0.3	0.320 (0.074)	0.344 (0.059)	0.294 (0.039)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		28.17	29.06	11.04

when the misidentification rate was as low as 0.025. However, for low capture probability cases, some negative bias was evident in the  $NE2_t$  estimators, and their performance was not as good as that of the  $M_t$  estimator (relative bias  $\approx 0.3 - 12\%$  and relative standard error  $\approx 5 - 15\%$  for cases 3 and 4).

## 4.3 Evolving Natural Tags

### 4.3.1 Proposed Misidentification Mechanisms

Although photographic tags based on natural marks that can change over time may have a risk of misidentification due to both types of errors, here we simplify the scenario, and consider only misidentification due to the second type of error, which is caused by change in natural marks over time. In other words, we here assume that the quality of photographs is high, and misidentification occurs only if the natural marks are modified or lost since the last capture event. We make the following assumptions:

1. Misidentification of an animal leads to creating a new but false identity;
2. Once a new identity is created, the old identity is not subject to recapture, but the new, false, identity is subject to recapture;
3. The same error is never repeated; and
4. Misidentification can occur only at recapture events.

These assumptions are similar to those for non-evolving natural tags 2. We assume that there is no risk of misidentification at the first capture event because misidentification occur in relation to comparison with previously existing natural marks (assumption 4). However, when changes occur in natural marks, the result is as if the original tag is lost and a new tag put in its place. Thus, misidentification leads to creating a new identity that persists, rather than a temporary false identification that cannot be repeated (assumption 2). We also assume that the new tag created by misidentification is different from tags on animals that already exist in the population (assumption 1), and that misidentification of two different animals never leads to the same new false identity (assumption 3).

The main difference between the misidentification mechanism associated with evolving natural tags, compared to the non-evolving natural tags, is that the original capture history, which is referred to as the real capture history, can not have any future recapture events once misidentification occurs, whereas the ghost capture history, that is created by misidentification, has the possibility of future recapture until further changes in the natural mark lead to occurrence of a new misidentification. This situation is comparable to that where a marked animal with an applied tag loses the tag, and is fitted with a new tag at a subsequent capture event. Thus, we never capture the animal with the original tag, but the animal may be recaptured with the newly applied tag. The terms of real and ghost capture histories have a different meaning from that in the non-evolving cases, but we continue using our original terminology for simplicity. We refer to this type of misidentification mechanism as *evolving natural tags*, and the model developed for data that contain this type of misidentification is denoted as *EV*.

In summary the misidentification mechanism for evolving natural tags has the following characteristics:

- Misidentification can occur at any recapture event;
- If a recaptured animal is incorrectly identified, the recapture event of that animal appears as a non-capture (i.e., the "real" capture history is recorded as [0]), but it also creates a capture history of a new animal in the population as a mirror image (i.e., a "ghost" capture history is created by recording the capture event [1] for the sampling occasion); and
- Once misidentification occurs, the "real" capture history cannot contain further recaptures, whereas the "ghost" capture history can be recaptured in the future until misidentification occurs again.

### 4.3.2 Statistical Model Development

We again use a 3-sample study on a closed population as an example. Terms and notations used follow those given in the previous chapters (see Tables 1.1 and 2.1). We have a parameter for capture probability of an animal at each sampling occasion,  $p_1$ ,  $p_2$  and  $p_3$ . Also, for simplicity, assuming that the probability of correct identification at recapture is constant for all animals throughout the study, we let  $\beta$  represent this probability. Notice that this parameter  $\beta$  applies

only to recaptured animals, and that  $(1 - \beta)$  can also be considered as the probability that the existing natural mark undergoes a change between two consecutive capture events. Consider an animal which is captured at all sampling occasions. The animal has true capture history [111], but has several possibilities for the observable capture histories depending on whether misidentification occurs. One of the possibilities is the pair of [100 ; 011], corresponding to the case where misidentification occurred only at the second sampling occasion, or in other words, the change in the natural mark occurred between the first and second sampling occasions. Given that an animal has a true capture history [111], the probability of observing the animal with real capture history [100] is  $p_1 p_2 (1 - \beta) p_3 \beta$ . This event also creates a ghost capture history [011], which has the same probability  $p_1 p_2 (1 - \beta) p_3 \beta$  because of the relationship between the real and ghost capture histories. Note that real capture history [100] did not have the possibility of recapture at the third sampling occasion because misidentification occurred at the second sampling occasion whereas the ghost capture history had the possibility of recapture at the third sampling occasions. Table 4.11 presents all the observable capture histories conditioned on the true capture history, and the probability of occurrence for the 3-sample case. The marginal probabilities for the observable capture histories in the 3-sample case are also summarized in Table 4.12 where  $P'_i = p_i \beta$  and  $Q'_i = (1 - p_i) Q'_{i+1} + p_i (1 - \beta)$  with  $Q'_{K+1} = 1$ . Notice that  $Q'_i$  here is defined differently from the other misidentification models, and again, the same issue arises; the total probability exceeds 1 because of the ghost capture histories created, and it equals 1 if and only if no misidentification occurs (i.e.,  $\beta = 1$ ).

Let  $t_1(\gamma)$  and  $t_2(\gamma)$  be the sampling occasions where the first and last, respectively, capture occurs for a given capture history  $\gamma$ . Then the general expression for the probability of each observable capture history  $\gamma$  for the study with  $K$ -sampling occasions is

$$\Pr[\gamma] = \left[ \prod_{i=1}^{t_1(\gamma)} p_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} \right] \left[ \prod_{i=t_1(\gamma)+1}^{t_2(\gamma)} P_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} \right]^h Q'_{t_2(\gamma)+1}$$

Table 4.11: A summary of the observable capture histories and associated probabilities for evolving natural tags for the 3-sample case.

$\omega$ (true history)	misID	$\gamma$ (observed history)	status	$\Pr[\gamma   \omega]$	
111	none	111	real	$p_1 p_2 \beta p_3 \beta$	
		at third	110	real	$p_1 p_2 \beta p_3 (1 - \beta)$
			001	ghost*	$p_1 p_2 \beta p_3 (1 - \beta)$
	at second	100	real	$p_1 p_2 (1 - \beta) p_3 \beta$	
		011	ghost*	$p_1 p_2 (1 - \beta) p_3 \beta$	
	at second and third	100	real	$p_1 p_2 (1 - \beta) p_3 (1 - \beta)$	
		010	ghost*	$p_1 p_2 (1 - \beta) p_3 (1 - \beta)$	
		001	ghost*	$p_1 p_2 (1 - \beta) p_3 (1 - \beta)$	
	110	none	110	real	$p_1 p_2 \beta (1 - p_3)$
100			real	$p_1 p_2 (1 - \beta) (1 - p_3)$	
at second		010	ghost*	$p_1 p_2 (1 - \beta) (1 - p_3)$	
101	none	101	real	$p_1 (1 - p_2) p_3 \beta$	
		at third	100	real	$p_1 (1 - p_2) p_3 (1 - \beta)$
	001		ghost*	$p_1 (1 - p_2) p_3 (1 - \beta)$	
100	none	100	real	$p_1 (1 - p_2) (1 - p_3)$	
011	none	011	real	$(1 - p_1) p_2 p_3 \beta$	
		third	010	real	$(1 - p_1) p_2 p_3 (1 - \beta)$
	001		ghost*	$(1 - p_1) p_2 p_3 (1 - \beta)$	
010	none	010	real	$(1 - p_1) p_2 (1 - p_3)$	
001	none	001	real	$(1 - p_1) (1 - p_2) p_3$	
000	none	000	real	$(1 - p_1) (1 - p_2) (1 - p_3)$	

Table 4.12: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for evolving natural tags in a 3-sample study.

$\gamma$ (observed history)	$\Pr[\gamma]$
111	$p_1 P'_2 P'_3$
110	$p_1 P'_2 Q'_3$
101	$p_1 q_2 P'_3$
100	$p_1 Q'_2$
011	$q_1 p_2 P'_3 + p_1 p_2 (1 - \beta) P'_3$
010	$q_1 p_2 Q'_3 + p_1 p_2 (1 - \beta) Q'_3$
001	$q_1 q_2 p_3 + (q_1 p_2 + p_1) p_3 (1 - \beta)$
000	$q_1 q_2 q_3$
Total**	$1 + [p_1 p_2 P'_3 + p_1 p_2 Q'_3 + q_1 p_2 p_3 + p_1 p_3](1 - \beta)$

\*\* Total = 1 if and only if  $\beta = 1$ .for  $\gamma$  with  $t_1(\gamma) = 1$ , and

$$\Pr[\gamma] = \left[ \prod_{i=1}^{t_1(\gamma)} p_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} + \sum_{i=1}^{t_1(\gamma)-1} \left( \prod_{j=0}^{i-1} (1 - p_j) p_i \right) p_{t_1(\gamma)} (1 - \beta) \right] \times \left[ \prod_{i=t_1(\gamma)+1}^{t_2(\gamma)} P_i^{\gamma_i} (1 - p_i)^{(1-\gamma_i)} \right]^h Q'_{t_2(\gamma)+1}$$

for  $\gamma$  with  $t_1(\gamma) > 1$  where $\gamma_i$  is the  $i$ th entry of capture history  $\gamma$  $p_i$  is the capture probability of an animal at the  $i$ th sampling occasion;  $p_j = 0$  if  $j = 0$  $\beta$  is the probability of correct identification

$$\begin{aligned}
P'_i &= p_i \beta \\
Q'_i &= (1 - p_i) Q'_{i+1} + p_i (1 - \beta) ; Q'_{K+1} = 1 \\
h &= 0 \text{ if } t_1(\gamma) = t_2(\gamma) ; \text{ else } h = 1.
\end{aligned}$$

### 4.3.3 Estimation

As for non-evolving natural tags, the typical multinomial approach to building a likelihood is invalid because of the dependency between pairs of real and ghost histories (which leads to the total probability exceeding 1). We again apply the methods of unweighted least squares and minimum  $\chi^2$ , which are based on using the observed values and marginal expected values of  $\mathbf{X}_\gamma$  to obtain estimates. The marginal expected values of  $\mathbf{X}_\gamma$  for the 3-sample case can be written as

$$\begin{aligned}
E[X_{111}] &= N [p_1 P'_2 P'_3] \\
E[X_{110}] &= N [p_1 P'_2 Q'_3] \\
E[X_{101}] &= N [p_1 q_2 P'_3] \\
E[X_{100}] &= N [p_1 Q'_2] \\
E[X_{011}] &= N [q_1 p_2 P'_3 + p_1 p_2 (1 - \beta) P'_3] \\
E[X_{010}] &= N [q_1 p_2 Q'_3 + p_1 p_2 (1 - \beta) Q'_3] \\
E[X_{001}] &= N [q_1 q_2 p_3 + (q_1 p_2 + p_1) p_3 (1 - \beta)] \\
E[X_{000}] &= N [q_1 q_2 q_3] .
\end{aligned}$$

where  $X_{000}$  is not observed. Then, the estimates are obtained by minimizing the quadratic distance function

$$\mathcal{F}_{ls} = \sum_{\gamma, \gamma \neq 000} (x_\gamma - E[X_\gamma])^2$$

or

$$\mathcal{F}_{\chi^2} = \sum_{\gamma, \gamma \neq 000} \frac{(x_\gamma - E[X_\gamma])^2}{E[X_\gamma]}$$

where  $x_\gamma$  represents the data and  $X_\gamma$  represents the random variable.

The method can also be conditioned on the total number of capture histories observed,  $X_{all}$ .

The total probability associated with the observed capture histories is

$$\begin{aligned}
 p^* &= 1 - q_1 q_2 q_3 + [p_1 p_2 P'_3 + p_1 p_2 Q'_3 + q_1 p_2 p_3 + p_1 p_3] (1 - \beta) \\
 &= 1 - q_1 q_2 q_3 + [p_1 p_2 + q_1 p_2 p_3 + p_1 p_3] (1 - \beta) \\
 &= 1 - q_1 q_2 q_3 + [q_1 q_2 q_3 - 1 + p_1 + p_2 + p_3] (1 - \beta)
 \end{aligned}$$

for the 3-sample study case, or in general,

$$p^* = 1 - \prod_{i=1}^K (1 - p_i) + \left[ \prod_{i=1}^K (1 - p_i) - 1 + \sum_{i=1}^K p_i \right] (1 - \beta)$$

for the  $K$ -sample case. Then expected values of  $\mathbf{X}_\gamma$  with the conditional approach can be written as

$$E[X_\gamma | X_{all} = x_{all}] = \frac{x_{all} \Pr[\gamma]}{p^*}$$

where  $x_{all}$  is the total number of capture histories observed. Then, the estimates are obtained by minimizing the quadratic distance function  $\mathcal{F}_{ls}$  or  $\mathcal{F}_{\chi^2}$  as described for the unconditional approach. With the conditional approach, the parameter  $N$  is removed from the estimation process and it is estimated as a derived parameter,

$$\hat{N} = \frac{x_{all}}{\hat{p}^*}.$$

#### 4.3.4 Simulation Study

##### Simulation 1: Cases with Time Specific Capture Probabilities

In our simulation study, we again considered a closed population of  $N$  animals, and a study with  $K = 5$  sampling occasions. We allowed for the capture probability to be time specific, and each animal was subject to capture with probability  $p_i$  at each sampling occasion  $i$ . When an animal was captured for the first time, the animal was not subject to misidentification. However, whenever an animal was recaptured, identification of the animal was either correct with probability  $\beta$ , or incorrect with probability  $(1 - \beta)$ . If the identification was correct, the event was recorded in the real capture history of the animal as a capture (i.e., [1]). However, if the identification was incorrect, the event was recorded as non-capture (i.e., [0]) in the real capture history, and a ghost capture

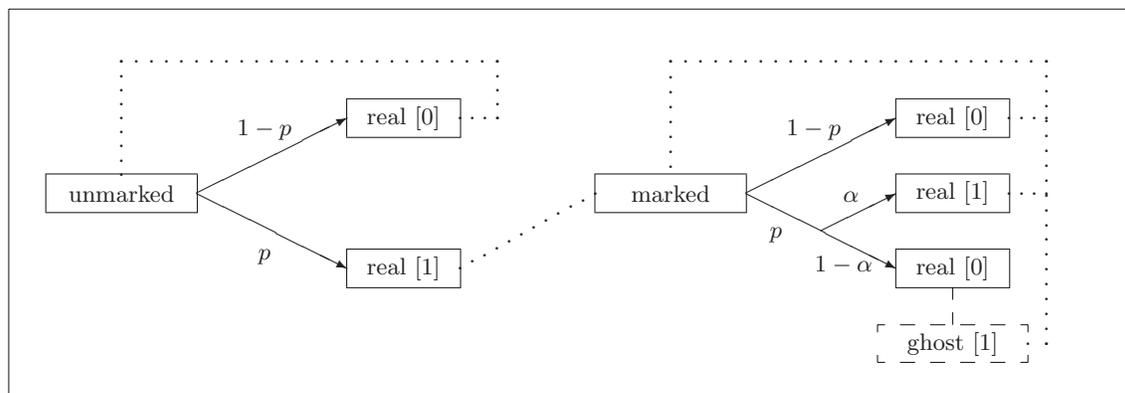


Figure 4.2: A diagram of the misidentification mechanism for evolving natural tags.

history was created with a capture recorded for the sampling occasion (i.e., [1]). Then, each animal was subject to capture at the next sampling occasion (see Figure 4.2). Note that "real" and "ghost" capture histories here have different meaning from those in non-evolving natural tags, and a "real" capture history does not have possibility of recapture once misidentification occurs. However, the "ghost" capture history will have possibility of recapture until another misidentification occurs.

We considered the same four specific cases as described in the previous section, and for each case, the correct identification rates of  $\beta = 0.7, 0.8, \text{ and } 0.9$  were considered.

$$\text{Case 1: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 2: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.7, 0.8, 0.7, 0.8, 0.7]$$

$$\text{Case 3: } N = 1000 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$$

$$\text{Case 4: } N = 200 \quad \text{and} \quad \mathbf{p} = [0.3, 0.2, 0.3, 0.2, 0.3]$$

As for non-evolving natural tags, we considered estimators based on the methods of unweighted least squares and minimum  $\chi^2$ , that is based on the quadratic distance functions of  $\mathcal{F}_{ls}$  and  $\mathcal{F}_{\chi^2}$ , respectively. In addition, unconditional and conditional (on  $x_{all}$ ) approaches were considered, and for each generated data set, estimates were obtained under our EV model (**Model EV<sub>t</sub>**) as well as using maximum likelihood (conditional on  $x_{all}$ ) under the conventional capture-recapture model (**Model M<sub>t</sub>**).

The performance of each estimator was again assessed by examining the average estimates, standard errors and root mean square errors of  $\hat{N}$  over 100 simulated data sets. The results for cases 1 to 4 are summarized in Tables 4.13 - 4.16. Although we considered both unconditional and conditional (on  $x_{all}$ ) approaches under Model  $EV_t$ , the unconditional approach again displayed numerical problems such as sensitivity to starting values and non-convergence. Thus, only results from the conditional (on  $x_{all}$ ) approach are presented in the Tables.

Here we observed the same tendency in the estimates of  $N$  as the cases for non-evolving natural tags, that is positive bias in  $\hat{N}$  if the misidentification was ignored, and the magnitude of the bias was substantial when the misidentification rate was high (relative bias  $> 50\%$  for  $\alpha = 0.07$  cases). The performance of estimators under Model  $EV_t$  was good, especially for the cases of high capture probability (relative bias  $\leq 2\%$  and relative standard error  $< 3\%$  for cases 1 and 2). However, again, some bias in  $\hat{N}$  were noted for the cases of low capture probability (relative bias  $\approx 1 - 10\%$  and relative standard error  $\approx 11 - 33\%$  for cases 3 and 4). Such bias in  $\hat{N}$  could be negative or positive depending on the case. The magnitude of bias and precision were better than in the cases with non-evolving natural tags 1 and similar to those with non-evolving natural tags 2. This is as expected because misidentification cannot occur on the first capture event here, and thus there are fewer occasions that misidentification can occur than in NE1, or about the same number of occasions in NE2. One interesting aspect is that the estimates of  $\hat{N}$  under Model  $M_t$  were exactly the same for the data generated under the two misidentification models, non-evolving natural tags 2 and evolving natural tags. This is because, at each sampling occasion, the total number of captures generated is the same under the NE2 and EV mechanisms (provided the same seed is used for the random number generator). The observed histories,  $X_\gamma$ , generated by the two mechanisms will differ, but the summary statistics used by the  $M_t$  estimator are the same. Hence, the estimates obtained under Model  $M_t$  were identical for the generated capture histories under two different misidentification mechanisms (NE2 and EV).

### **Simulation 2: Cases with Time Specific Capture Probabilities (High $\alpha$ )**

We also considered the cases of lower misidentification rates. We generated new sets of data for the four cases described in the previous section, but with correct identification rates of  $\beta = 0.950, 0.975$  and  $1.000$ , and the data sets were analyzed by using the two estimation methods, the

Table 4.13: [Simulation 1: case 1] Evolving natural tags with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	999 (12)	1006 (11)	2011 (41)
$\beta$	0.7	0.700 (0.010)	0.702 (0.010)	--
$p_1$	0.7	0.698 (0.020)	0.694 (0.017)	0.347 (0.010)
$p_2$	0.8	0.801 (0.018)	0.798 (0.019)	0.399 (0.010)
$p_3$	0.7	0.696 (0.019)	0.695 (0.018)	0.347 (0.010)
$p_4$	0.8	0.800 (0.018)	0.796 (0.017)	0.398 (0.010)
$p_5$	0.7	0.701 (0.018)	0.699 (0.018)	0.349 (0.010)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		12.04	12.52	1011.83
$N$	1000	1001 (10)	1004 (9)	1614 (28)
$\beta$	0.8	0.800 (0.009)	0.801 (0.009)	--
$p_1$	0.7	0.696 (0.018)	0.696 (0.017)	0.432 (0.012)
$p_2$	0.8	0.800 (0.018)	0.796 (0.017)	0.496 (0.011)
$p_3$	0.7	0.700 (0.018)	0.698 (0.016)	0.434 (0.011)
$p_4$	0.8	0.800 (0.015)	0.796 (0.015)	0.496 (0.011)
$p_5$	0.7	0.700 (0.015)	0.698 (0.016)	0.434 (0.012)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		10.04	9.84	614.63
$N$	1000	999 (7)	1000 (8)	1287 (16)
$\beta$	0.9	0.900 (0.006)	0.900 (0.006)	--
$p_1$	0.7	0.700 (0.018)	0.698 (0.017)	0.543 (0.014)
$p_2$	0.8	0.800 (0.014)	0.799 (0.013)	0.622 (0.012)
$p_3$	0.7	0.697 (0.019)	0.696 (0.015)	0.542 (0.013)
$p_4$	0.8	0.802 (0.015)	0.799 (0.014)	0.623 (0.011)
$p_5$	0.7	0.703 (0.018)	0.701 (0.015)	0.546 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	8.00	287.44

Table 4.14: [Simulation 1: case 2] Evolving natural tags with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	199 (5)	204 (5)	401 (17)
$\beta$	0.7	0.699 (0.021)	0.710 (0.020)	--
$p_1$	0.7	0.700 (0.042)	0.688 (0.034)	0.349 (0.021)
$p_2$	0.8	0.801 (0.038)	0.787 (0.036)	0.400 (0.024)
$p_3$	0.7	0.696 (0.039)	0.688 (0.035)	0.348 (0.021)
$p_4$	0.8	0.794 (0.037)	0.782 (0.037)	0.397 (0.022)
$p_5$	0.7	0.697 (0.049)	0.690 (0.036)	0.348 (0.023)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		5.09	6.40	201.71
$N$	200	199 (4)	202 (4)	323 (12)
$\beta$	0.8	0.799 (0.019)	0.804 (0.018)	--
$p_1$	0.7	0.702 (0.038)	0.693 (0.035)	0.433 (0.024)
$p_2$	0.8	0.798 (0.034)	0.783 (0.035)	0.493 (0.025)
$p_3$	0.7	0.705 (0.044)	0.696 (0.040)	0.435 (0.028)
$p_4$	0.8	0.804 (0.034)	0.790 (0.034)	0.497 (0.025)
$p_5$	0.7	0.704 (0.039)	0.697 (0.035)	0.435 (0.025)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.12	4.47	123.58
$N$	200	200 (4)	200 (4)	257 (7)
$\beta$	0.9	0.900 (0.015)	0.900 (0.013)	--
$p_1$	0.7	0.699 (0.040)	0.694 (0.034)	0.544 (0.025)
$p_2$	0.8	0.798 (0.035)	0.787 (0.033)	0.621 (0.028)
$p_3$	0.7	0.698 (0.039)	0.693 (0.034)	0.543 (0.029)
$p_4$	0.8	0.799 (0.039)	0.789 (0.032)	0.621 (0.029)
$p_5$	0.7	0.706 (0.043)	0.699 (0.035)	0.547 (0.029)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.00	4.00	57.42

Table 4.15: [Simulation 1: case 3] Evolving natural tags with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1019 (184)	985 (141)	1568 (65)
$\beta$	0.7	0.711 (0.094)	0.706 (0.076)	--
$p_1$	0.3	0.304 (0.053)	0.312 (0.045)	0.191 (0.013)
$p_2$	0.2	0.203 (0.039)	0.211 (0.032)	0.128 (0.009)
$p_3$	0.3	0.303 (0.057)	0.312 (0.046)	0.191 (0.011)
$p_4$	0.2	0.202 (0.038)	0.213 (0.033)	0.129 (0.009)
$p_5$	0.3	0.307 (0.055)	0.317 (0.043)	0.194 (0.012)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		184.97	141.79	571.70
$N$	1000	1016 (156)	967 (128)	1326 (47)
$\beta$	0.8	0.811 (0.096)	0.796 (0.082)	--
$p_1$	0.3	0.303 (0.052)	0.319 (0.047)	0.227 (0.012)
$p_2$	0.2	0.202 (0.037)	0.216 (0.033)	0.152 (0.011)
$p_3$	0.3	0.302 (0.050)	0.319 (0.044)	0.227 (0.014)
$p_4$	0.2	0.200 (0.035)	0.215 (0.033)	0.151 (0.012)
$p_5$	0.3	0.302 (0.048)	0.318 (0.043)	0.227 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		156.81	132.18	329.37
$N$	1000	1010 (114)	979 (112)	1150 (34)
$\beta$	0.9	0.905 (0.076)	0.894 (0.074)	--
$p_1$	0.3	0.302 (0.036)	0.314 (0.039)	0.262 (0.014)
$p_2$	0.2	0.200 (0.026)	0.211 (0.026)	0.174 (0.013)
$p_3$	0.3	0.300 (0.039)	0.312 (0.039)	0.261 (0.014)
$p_4$	0.2	0.202 (0.028)	0.212 (0.028)	0.175 (0.013)
$p_5$	0.3	0.300 (0.040)	0.311 (0.039)	0.260 (0.015)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		114.43	113.95	153.80

Table 4.16: [Simulation 1: case 4] Evolving natural tags with time specific capture probabilities. Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	209 (65)	180 (39)	309 (27)
$\beta$	0.7	0.735 (0.163)	0.707 (0.114)	--
$p_1$	0.3	0.305 (0.102)	0.352 (0.080)	0.191 (0.026)
$p_2$	0.2	0.212 (0.072)	0.255 (0.060)	0.134 (0.024)
$p_3$	0.3	0.320 (0.105)	0.365 (0.081)	0.198 (0.022)
$p_4$	0.2	0.214 (0.070)	0.250 (0.056)	0.132 (0.022)
$p_5$	0.3	0.318 (0.107)	0.364 (0.090)	0.198 (0.025)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		65.62	43.82	112.29
$N$	200	213 (55)	186 (40)	271 (19)
$\beta$	0.8	0.826 (0.161)	0.794 (0.128)	--
$p_1$	0.3	0.295 (0.084)	0.344 (0.076)	0.221 (0.027)
$p_2$	0.2	0.203 (0.066)	0.242 (0.059)	0.149 (0.024)
$p_3$	0.3	0.300 (0.087)	0.345 (0.083)	0.220 (0.031)
$p_4$	0.2	0.199 (0.065)	0.243 (0.064)	0.148 (0.022)
$p_5$	0.3	0.304 (0.099)	0.344 (0.079)	0.221 (0.027)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		56.51	42.37	73.49
$N$	200	197 (39)	180 (33)	230 (14)
$\beta$	0.9	0.885 (0.128)	0.867 (0.110)	--
$p_1$	0.3	0.318 (0.086)	0.354 (0.072)	0.263 (0.032)
$p_2$	0.2	0.210 (0.064)	0.244 (0.055)	0.173 (0.024)
$p_3$	0.3	0.321 (0.077)	0.355 (0.078)	0.263 (0.035)
$p_4$	0.2	0.213 (0.060)	0.246 (0.058)	0.175 (0.026)
$p_5$	0.3	0.317 (0.089)	0.351 (0.079)	0.261 (0.036)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		39.11	38.58	33.10

methods of unweighted least squares and minimum  $\chi^2$ , under Model  $EV_t$  and maximum likelihood (conditional on  $x_{all}$ ) under Model  $M_t$ . The results for cases 1 to 4 are summarized in Tables 4.17 - 4.20. The unconditional approach under Model  $EV_t$  had numerical problems. Thus, we only included the results from the conditional (on  $x_{all}$ ) approach in the Tables.

Again, we observed the same tendency; the performance of the  $M_t$  estimator improved as the value of  $\beta$  increased. However, there was still some positive bias in  $\hat{N}$  if misidentification is present, even when the misidentification rate was as low as 0.025 (relative bias  $> 5\%$  and  $3\%$  for  $\alpha = 0.950$  and  $0.975$ , respectively). For high capture probability cases, the  $EV_t$  estimators perform well (relative bias  $< 1\%$  and relative standard error  $< 2\%$  for cases 1 and 2). However, for low capture probability cases, some negative bias was noted in  $\hat{N}$ , especially for case 4 with minimum  $\chi^2$  (relative bias  $\approx 10 - 13\%$  and relative standard error  $\approx 12 - 14\%$ ). Also, the performance of estimators under Model  $EV_t$  was not as good as the performance of the Model  $M_t$  estimator for low capture probability cases.

## 4.4 Discussion

For both non-evolving natural tags 2 and evolving natural tags, we observed the same tendencies in performance of the estimators. The  $\hat{N}$  were positively biased if misidentification was ignored, and the bias could be substantial if the misidentification rate was high. In general, the estimators under Model NE2 and Model EV performed well for the cases with high capture probability. However, estimators of  $\hat{N}$  had substantial bias for the cases of low capture probability, and the bias tended to be negative for the low misidentification cases. Also, cases with misidentification rates as low as 0.025, the performance of the NE2 and EV estimators was not as good as that of the Model  $M_t$  estimator, especially for low capture probability cases. It is probably a reasonable observation that as capture probability becomes lower, we do not capture enough animals to have enough information to estimate the correct identification rate in addition to the capture probabilities, and the simpler model, Model  $M_t$ , has advantages. In addition, as the correct identification rate increases, the capture-recapture data contain fewer misidentifications. Consequently, data do not contain much information on the misidentification rate.

In this chapter, we focused on two factors that can lead to misidentification in photographic tag-based capture-recapture studies: poor quality of photographs and changes in natural marks.

Table 4.17: [Simulation 2: case 1] Evolving natural tags with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	1000 (8)	1001 (6)	1139 (11)
$\beta$	0.950	0.950 (0.005)	0.950 (0.005)	--
$p_1$	0.7	0.697 (0.019)	0.695 (0.015)	0.612 (0.014)
$p_2$	0.8	0.799 (0.018)	0.796 (0.014)	0.702 (0.011)
$p_3$	0.7	0.700 (0.018)	0.698 (0.015)	0.615 (0.014)
$p_4$	0.8	0.800 (0.015)	0.797 (0.014)	0.702 (0.013)
$p_5$	0.7	0.700 (0.018)	0.698 (0.015)	0.614 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		8.00	6.08	139.43
$N$	1000	999 (7)	998 (6)	1068 (8)
$\beta$	0.975	0.975 (0.004)	0.974 (0.004)	--
$p_1$	0.7	0.699 (0.020)	0.697 (0.016)	0.653 (0.015)
$p_2$	0.8	0.800 (0.014)	0.798 (0.013)	0.749 (0.013)
$p_3$	0.7	0.697 (0.019)	0.696 (0.014)	0.653 (0.014)
$p_4$	0.8	0.802 (0.015)	0.799 (0.014)	0.750 (0.013)
$p_5$	0.7	0.702 (0.020)	0.701 (0.015)	0.657 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		7.07	6.32	68.46
$N$	1000	998 (4)	999 (3)	1001 (1)
$\beta$	1.000	0.999 (0.001)	0.999 (0.001)	--
$p_1$	0.7	0.702 (0.018)	0.698 (0.014)	0.699 (0.014)
$p_2$	0.8	0.801 (0.014)	0.798 (0.012)	0.801 (0.012)
$p_3$	0.7	0.700 (0.016)	0.698 (0.014)	0.699 (0.014)
$p_4$	0.8	0.799 (0.016)	0.797 (0.013)	0.799 (0.013)
$p_5$	0.7	0.701 (0.016)	0.698 (0.013)	0.699 (0.013)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		4.47	3.16	1.41

Table 4.18: [Simulation 2: case 2] Evolving natural tags with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	199 (3)	199 (3)	228 (5)
$\beta$	0.950	0.950 (0.012)	0.949 (0.011)	--
$p_1$	0.7	0.697 (0.040)	0.692 (0.031)	0.613 (0.029)
$p_2$	0.8	0.797 (0.036)	0.783 (0.030)	0.698 (0.028)
$p_3$	0.7	0.702 (0.045)	0.696 (0.039)	0.616 (0.034)
$p_4$	0.8	0.802 (0.033)	0.790 (0.032)	0.704 (0.028)
$p_5$	0.7	0.705 (0.041)	0.696 (0.034)	0.616 (0.030)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	3.16	28.44
$N$	200	199 (3)	199 (3)	214 (3)
$\beta$	0.975	0.974 (0.009)	0.973 (0.009)	--
$p_1$	0.7	0.704 (0.042)	0.695 (0.033)	0.654 (0.030)
$p_2$	0.8	0.797 (0.032)	0.787 (0.030)	0.747 (0.030)
$p_3$	0.7	0.698 (0.039)	0.693 (0.032)	0.653 (0.031)
$p_4$	0.8	0.800 (0.037)	0.787 (0.032)	0.746 (0.030)
$p_5$	0.7	0.704 (0.045)	0.696 (0.032)	0.658 (0.030)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		3.16	3.16	14.31
$N$	200	199 (2)	199 (1)	201 (1)
$\beta$	1.000	0.997 (0.004)	0.998 (0.003)	--
$p_1$	0.7	0.709 (0.044)	0.696 (0.036)	0.703 (0.036)
$p_2$	0.8	0.802 (0.033)	0.789 (0.026)	0.800 (0.028)
$p_3$	0.7	0.697 (0.041)	0.691 (0.032)	0.696 (0.033)
$p_4$	0.8	0.804 (0.034)	0.790 (0.029)	0.801 (0.030)
$p_5$	0.7	0.700 (0.045)	0.692 (0.031)	0.697 (0.033)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		2.23	1.41	1.41

Table 4.19: [Simulation 2: case 3] Evolving natural tags with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	1000	979 (93)	954 (84)	1069 (32)
$\beta$	0.950	0.936 (0.064)	0.927 (0.060)	--
$p_1$	0.3	0.311 (0.039)	0.320 (0.035)	0.282 (0.015)
$p_2$	0.2	0.208 (0.027)	0.216 (0.025)	0.188 (0.013)
$p_3$	0.3	0.310 (0.036)	0.320 (0.034)	0.281 (0.016)
$p_4$	0.2	0.205 (0.027)	0.216 (0.025)	0.188 (0.014)
$p_5$	0.3	0.308 (0.036)	0.319 (0.033)	0.281 (0.014)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		95.34	95.77	76.05
$N$	1000	972 (70)	959 (75)	1032 (27)
$\beta$	0.975	0.957 (0.051)	0.954 (0.054)	--
$p_1$	0.3	0.311 (0.026)	0.318 (0.029)	0.292 (0.015)
$p_2$	0.2	0.207 (0.021)	0.214 (0.021)	0.194 (0.014)
$p_3$	0.3	0.311 (0.028)	0.316 (0.030)	0.290 (0.015)
$p_4$	0.2	0.209 (0.021)	0.214 (0.022)	0.195 (0.014)
$p_5$	0.3	0.309 (0.030)	0.316 (0.030)	0.290 (0.017)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		75.39	85.47	41.86
$N$	1000	965 (61)	948 (58)	1001 (22)
$\beta$	1.000	0.974 (0.041)	0.968 (0.041)	--
$p_1$	0.3	0.315 (0.030)	0.323 (0.026)	0.303 (0.016)
$p_2$	0.2	0.209 (0.020)	0.216 (0.020)	0.200 (0.014)
$p_3$	0.3	0.314 (0.027)	0.319 (0.025)	0.299 (0.017)
$p_4$	0.2	0.207 (0.023)	0.214 (0.020)	0.199 (0.014)
$p_5$	0.3	0.312 (0.029)	0.321 (0.026)	0.301 (0.016)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		70.32	77.89	22.02

Table 4.20: [Simulation 2: case 4] Evolving natural tags with time specific capture probabilities (high  $\alpha$ ). Average estimates (with standard errors in parentheses) based on 100 simulated data sets. Estimates under Model  $EV_t$  are from the conditional (on  $x_{all}$ ) approach.

		Model $EV_t$		Model $M_t$
		least squares	minimum $\chi^2$	conditional $\mathcal{L}$
$N$	200	190 (32)	179 (27)	216 (13)
$\beta$	0.950	0.908 (0.104)	0.899 (0.092)	--
$p_1$	0.3	0.318 (0.066)	0.349 (0.060)	0.277 (0.033)
$p_2$	0.2	0.223 (0.055)	0.246 (0.050)	0.187 (0.030)
$p_3$	0.3	0.328 (0.075)	0.350 (0.070)	0.276 (0.037)
$p_4$	0.2	0.216 (0.053)	0.247 (0.055)	0.185 (0.029)
$p_5$	0.3	0.326 (0.081)	0.350 (0.067)	0.276 (0.034)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		33.52	34.20	20.61
$N$	200	188 (29)	177 (25)	207 (10)
$\beta$	0.975	0.928 (0.100)	0.918 (0.087)	--
$p_1$	0.3	0.328 (0.074)	0.356 (0.061)	0.292 (0.035)
$p_2$	0.2	0.216 (0.056)	0.245 (0.049)	0.192 (0.025)
$p_3$	0.3	0.333 (0.066)	0.357 (0.068)	0.292 (0.039)
$p_4$	0.2	0.220 (0.053)	0.247 (0.050)	0.195 (0.028)
$p_5$	0.3	0.325 (0.075)	0.353 (0.066)	0.289 (0.038)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		31.38	33.97	12.20
$N$	200	185 (27)	177 (25)	203 (11)
$\beta$	1.000	0.939 (0.092)	0.930 (0.087)	--
$p_1$	0.3	0.341 (0.081)	0.364 (0.073)	0.303 (0.039)
$p_2$	0.2	0.225 (0.053)	0.252 (0.047)	0.202 (0.027)
$p_3$	0.3	0.336 (0.071)	0.358 (0.067)	0.297 (0.036)
$p_4$	0.2	0.226 (0.054)	0.245 (0.050)	0.196 (0.034)
$p_5$	0.3	0.327 (0.079)	0.352 (0.071)	0.293 (0.039)
no. not conv.		0	0	0
$\sqrt{\text{MSE}(\hat{N})}$		30.88	33.97	11.40

In general, in photographic tag-based capture-recapture studies, there could be a multiplicative effect of these two types of misidentification mechanisms. Although it may be necessary to have a more complex structure depending on the study, a simple way to consider both effects is to have probability of correct identification =  $\alpha\beta$ . For those studies that use non-evolving natural tags, we only need to consider misidentification risk due to poor quality of photographs (i.e., we can assume  $\beta = 1$ ), and Model NE2 is a reasonable model to analyze such data. Although we used an oversimplified scenario to develop a model for studies that use evolving natural tags (i.e., we assumed that  $\alpha = 1$ ), in reality, the misidentification issue for those studies is more complicated because neither  $\alpha$  nor  $\beta$  should be treated as 1. It is an important next step to develop a clear framework to analyze data that have both types of misidentification mechanisms, or develop study designs that can eliminate one or the other type of error.

Poor quality photographs are usually discarded in photographic tag-based capture-recapture studies, thus reducing the sample size and capture probabilities greatly. On the other hand, Models NE1 and NE2 allow for misidentification that is related to quality of photographs, thus marginal quality photographs can be included in capture-recapture study. Both misidentification mechanisms are applicable to photographic tag-based capture-recapture studies, and it is left for researchers to decide which misidentification mechanism is more likely in the study. It is an interesting future research topic to examine the cost and benefit of inclusion of marginal quality photographs.

Evolving natural tags have additional complicated aspects that need to be addressed in future research. For example, for evolving natural tags, it is more realistic to assume that the probability of misidentification is greater (i.e., smaller  $\beta$ ) for an animal that is not observed for a longer period of time because it gives more chance for natural marks to be modified or lost. We considered only the case that the probability of misidentification is constant for all sampling occasions and all animals to simplify the scenario in this chapter, and it is probably a reasonable assumption in closed population model time scale. However, one way to relax this assumption is to simply define  $\beta$  to be the probability that the existing natural mark undergoes a change between two sampling occasions rather than two consecutive capture events. For example, the probability of observing [101] given that true capture history would be [101] is  $p_1(1 - p_2)\beta p_3\beta$ . Alternatively, we can define the probability of correct identification in relation to the number of consecutive non-capture events: define parameters  $\beta_i$  where  $i$  indicates number of consecutive non-capture sampling occasions, and

assume that  $\beta_0 > \beta_1 > \dots > \beta_{K-2}$ . For example, the probability of observing an animal with capture history [111] given that the animal has true capture history [111] is  $p_1 p_2 \beta_0 p_3 \beta_0$  whereas that of [101] given that animal has true capture history [101] is  $p_1 (1 - p_2) p_3 \beta_1$ . On the other hand, if the probability of misidentification is greater for animals that are not observed for a longer period of time, then the effects of misidentification can be more serious with long-term studies. Extension of misidentification models to open population models, and relaxation of assumption of constant misidentification rate are also important future research topics, especially for evolving natural tags.

The conditional likelihood approach we considered in Chapter 3 can be applied to non-evolving natural tags in the same manner. However, the approach is not practical for evolving natural tags. The essence of the conditional likelihood approach is to eliminate ghost capture histories while minimizing the elimination of real capture histories. With evolving natural tags, ghost capture histories appear in all observed capture histories except for the ones that have capture event at the first sampling occasion (see Appendix A.1 - A.3). Consequently, elimination of ghost capture histories results in elimination of most part of data.

We here excluded the possibility that misidentification consists of assigning the identity of a different animal in the population to the captured animal. Considering the number of different DNA fingerprints that can be created through errors, there is a very small chance that a DNA fingerprint that is created by error will be the same as the true DNA fingerprint of another animal. Thus, it is a reasonable assumption for genetic tag-based capture-recapture studies. However, there seems to be a greater chance that misidentification may lead to identification of existing animals in the population with photographic tag-based studies. For example, visible natural marks of different animals may look similar, and such misidentification may lead to the false identification of an existing animal in the population. Also, changes in natural marks may not be obvious, thus both real and ghost capture histories of the animal could be recaptured in the future. These additional aspects are also interesting future research topics. In addition, photographic tag-based capture-recapture studies can also have a problem with multiple captures of an animal at a sampling occasion. For example, multiple photographs of an animals can be taken, and there is a risk of multiple misidentification of an animal, leading to creation of extra ghost capture histories. As indicated in Chapter 2, this problem with multiple captures is not covered under Models NE2 and EV, and this aspect needs to be investigated as a future research topic.

Finally, there has been a tendency to consider that misidentification issues with genetic tag-

and photographic tag-based capture-recapture studies are similar. However, there are differences in the misidentification mechanism, as we described. In addition, there are many factors that affect misidentification, such as types of natural tags used, species studied, study design applied, and so on. It is important to keep in mind that the misidentification mechanism can be very specific to the study, and effects on estimates can be substantial if it not appropriately accounted for.

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# Appendix

## Appendix A

# Summaries of the Marginal Probabilities in a 5-Sample Study

Table A.1: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for non-evolving natural tags 1 in a 5-sample study.

$\gamma$ (observed history)	$\Pr[\gamma]$					
11111	$P'_1$	$P'_2$	$P'_3$	$P'_4$	$P'_5$	
11110	$P'_1$	$P'_2$	$P'_3$	$P'_4$	$Q'_5$	
11101	$P'_1$	$P'_2$	$P'_3$	$Q'_4$	$P'_5$	
11100	$P'_1$	$P'_2$	$P'_3$	$Q'_4$	$Q'_5$	
11011	$P'_1$	$P'_2$	$Q'_3$	$P'_4$	$P'_5$	
11010	$P'_1$	$P'_2$	$Q'_3$	$P'_4$	$Q'_5$	
11001	$P'_1$	$P'_2$	$Q'_3$	$Q'_4$	$P'_5$	
11000	$P'_1$	$P'_2$	$Q'_3$	$Q'_4$	$Q'_5$	
10111	$P'_1$	$Q'_2$	$P'_3$	$P'_4$	$P'_5$	
10110	$P'_1$	$Q'_2$	$P'_3$	$P'_4$	$Q'_5$	
10101	$P'_1$	$Q'_2$	$P'_3$	$Q'_4$	$P'_5$	
10100	$P'_1$	$Q'_2$	$P'_3$	$Q'_4$	$Q'_5$	
10011	$P'_1$	$Q'_2$	$Q'_3$	$P'_4$	$P'_5$	
10010	$P'_1$	$Q'_2$	$Q'_3$	$P'_4$	$Q'_5$	
10001	$P'_1$	$Q'_2$	$Q'_3$	$Q'_4$	$P'_5$	
10000	$P'_1$	$Q'_2$	$Q'_3$	$Q'_4$	$Q'_5$	+ $p_1(1 - \alpha)$
01111	$Q'_1$	$P'_2$	$P'_3$	$P'_4$	$P'_5$	
01110	$Q'_1$	$P'_2$	$P'_3$	$P'_4$	$Q'_5$	
01101	$Q'_1$	$P'_2$	$P'_3$	$Q'_4$	$P'_5$	
01100	$Q'_1$	$P'_2$	$P'_3$	$Q'_4$	$Q'_5$	
01011	$Q'_1$	$P'_2$	$Q'_3$	$P'_4$	$P'_5$	
01010	$Q'_1$	$P'_2$	$Q'_3$	$P'_4$	$Q'_5$	
01001	$Q'_1$	$P'_2$	$Q'_3$	$Q'_4$	$P'_5$	
01000	$Q'_1$	$P'_2$	$Q'_3$	$Q'_4$	$Q'_5$	+ $p_2(1 - \alpha)$
00111	$Q'_1$	$Q'_2$	$P'_3$	$P'_4$	$P'_5$	
00110	$Q'_1$	$Q'_2$	$P'_3$	$P'_4$	$Q'_5$	
00101	$Q'_1$	$Q'_2$	$P'_3$	$Q'_4$	$P'_5$	
00100	$Q'_1$	$Q'_2$	$P'_3$	$Q'_4$	$Q'_5$	+ $p_3(1 - \alpha)$
00011	$Q'_1$	$Q'_2$	$Q'_3$	$P'_4$	$P'_5$	
00010	$Q'_1$	$Q'_2$	$Q'_3$	$P'_4$	$Q'_5$	+ $p_4(1 - \alpha)$
00001	$Q'_1$	$Q'_2$	$Q'_3$	$Q'_4$	$P'_5$	+ $p_5(1 - \alpha)$
00000	$Q'_1$	$Q'_2$	$Q'_3$	$Q'_4$	$Q'_5$	

Table A.2: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for non-evolving natural tags 2 in a 5-sample study.

$\gamma$ (observed history)						$\Pr[\gamma]$
11111	$p_1$	$P'_2$	$P'_3$	$P'_4$	$P'_5$	
11110	$p_1$	$P'_2$	$P'_3$	$P'_4$	$Q'_5$	
11101	$p_1$	$P'_2$	$P'_3$	$Q'_4$	$P'_5$	
11100	$p_1$	$P'_2$	$P'_3$	$Q'_4$	$Q'_5$	
11011	$p_1$	$P'_2$	$Q'_3$	$P'_4$	$P'_5$	
11010	$p_1$	$P'_2$	$Q'_3$	$P'_4$	$Q'_5$	
11001	$p_1$	$P'_2$	$Q'_3$	$Q'_4$	$P'_5$	
11000	$p_1$	$P'_2$	$Q'_3$	$Q'_4$	$Q'_5$	
10111	$p_1$	$Q'_2$	$P'_3$	$P'_4$	$P'_5$	
10110	$p_1$	$Q'_2$	$P'_3$	$P'_4$	$Q'_5$	
10101	$p_1$	$Q'_2$	$P'_3$	$Q'_4$	$P'_5$	
10100	$p_1$	$Q'_2$	$P'_3$	$Q'_4$	$Q'_5$	
10011	$p_1$	$Q'_2$	$Q'_3$	$P'_4$	$P'_5$	
10010	$p_1$	$Q'_2$	$Q'_3$	$P'_4$	$Q'_5$	
10001	$p_1$	$Q'_2$	$Q'_3$	$Q'_4$	$P'_5$	
10000	$p_1$	$Q'_2$	$Q'_3$	$Q'_4$	$Q'_5$	
01111	$(1 - p_1)$	$p_2$	$P'_3$	$P'_4$	$P'_5$	
01110	$(1 - p_1)$	$p_2$	$P'_3$	$P'_4$	$Q'_5$	
01101	$(1 - p_1)$	$p_2$	$P'_3$	$Q'_4$	$P'_5$	
01100	$(1 - p_1)$	$p_2$	$P'_3$	$Q'_4$	$Q'_5$	
01011	$(1 - p_1)$	$p_2$	$Q'_3$	$P'_4$	$P'_5$	
01010	$(1 - p_1)$	$p_2$	$Q'_3$	$P'_4$	$Q'_5$	
01001	$(1 - p_1)$	$p_2$	$Q'_3$	$Q'_4$	$P'_5$	
01000	$(1 - p_1)$	$p_2$	$Q'_3$	$Q'_4$	$Q'_5$	$+ p_1 p_2 (1 - \alpha)$
00111	$(1 - p_1) (1 - p_2)$	$p_3$	$P'_4$	$P'_5$		
00110	$(1 - p_1) (1 - p_2)$	$p_3$	$P'_4$	$Q'_5$		
00101	$(1 - p_1) (1 - p_2)$	$p_3$	$Q'_4$	$P'_5$		
00100	$(1 - p_1) (1 - p_2)$	$p_3$	$Q'_4$	$Q'_5$		$+ [p_1 + (1 - p_1)p_2]p_3(1 - \alpha)$
00011	$(1 - p_1) (1 - p_2) (1 - p_3)$	$p_4$	$P'_5$			
00010	$(1 - p_1) (1 - p_2) (1 - p_3)$	$p_4$	$Q'_5$			$+ [p_1 + (1 - p_1)p_2 + (1 - p_1)(1 - p_2)p_3]p_4(1 - \alpha)$
00001	$(1 - p_1) (1 - p_2) (1 - p_3) (1 - p_4)$	$p_5$				$+ [p_1 + (1 - p_1)p_2 + (1 - p_1)(1 - p_2)p_3 + (1 - p_1)(1 - p_2)(1 - p_3)p_4]p_5(1 - \alpha)$
00000	$(1 - p_1) (1 - p_2) (1 - p_3) (1 - p_4) (1 - p_5)$					

Table A.3: A summary of the marginal probabilities of the observable capture histories,  $\gamma$ , for evolving natural tags in a 5-sample study.

$\gamma$ (observed history)						$\Pr[\gamma]$
11111	$p_1$	$P'_2$	$P'_3$	$P'_4$	$P'_5$	
11110	$p_1$	$P'_2$	$P'_3$	$P'_4$	$Q'_5$	
11101	$p_1$	$P'_2$	$P'_3$	$Q'_4$	$P'_5$	
11100	$p_1$	$P'_2$	$P'_3$	$Q'_4$		
11011	$p_1$	$P'_2$	$Q'_3$	$P'_4$	$P'_5$	
11010	$p_1$	$P'_2$	$Q'_3$	$P'_4$	$Q'_5$	
11001	$p_1$	$P'_2$	$Q'_3$	$Q'_4$	$P'_5$	
11000	$p_1$	$P'_2$	$Q'_3$			
10111	$p_1$	$Q'_2$	$P'_3$	$P'_4$	$P'_5$	
10110	$p_1$	$Q'_2$	$P'_3$	$P'_4$	$Q'_5$	
10101	$p_1$	$Q'_2$	$P'_3$	$Q'_4$	$P'_5$	
10100	$p_1$	$Q'_2$	$P'_3$	$Q'_4$		
10011	$p_1$	$Q'_2$	$Q'_3$	$P'_4$	$P'_5$	
10010	$p_1$	$Q'_2$	$Q'_3$	$P'_4$	$Q'_5$	
10001	$p_1$	$Q'_2$	$Q'_3$	$Q'_4$	$P'_5$	
10000	$p_1$	$Q'_2$				
01111	$(1-p_1)$	$p_2$	$P'_3$	$P'_4$	$P'_5$	+ $p_1 p_2 (1-\alpha) P'_3 P'_4 P'_5$
01110	$(1-p_1)$	$p_2$	$P'_3$	$P'_4$	$Q'_5$	+ $p_1 p_2 (1-\alpha) P'_3 P'_4 Q'_5$
01101	$(1-p_1)$	$p_2$	$P'_3$	$Q'_4$	$P'_5$	+ $p_1 p_2 (1-\alpha) P'_3 Q'_4 P'_5$
01100	$(1-p_1)$	$p_2$	$P'_3$	$Q'_4$		+ $p_1 p_2 (1-\alpha) P'_3 Q'_4$
01011	$(1-p_1)$	$p_2$	$Q'_3$	$P'_4$	$P'_5$	+ $p_1 p_2 (1-\alpha) Q'_3 P'_4 P'_5$
01010	$(1-p_1)$	$p_2$	$Q'_3$	$P'_4$	$Q'_5$	+ $p_1 p_2 (1-\alpha) Q'_3 P'_4 Q'_5$
01001	$(1-p_1)$	$p_2$	$Q'_3$	$Q'_4$	$P'_5$	+ $p_1 p_2 (1-\alpha) Q'_3 Q'_4 P'_5$
01000	$(1-p_1)$	$p_2$	$Q'_3$			+ $p_1 p_2 (1-\alpha) Q'_3$
00111	$(1-p_1)(1-p_2)$	$p_3$	$P'_4$	$P'_5$		+ $[p_1 + (1-p_1)p_2] p_3 (1-\alpha) P'_4 P'_5$
00110	$(1-p_1)(1-p_2)$	$p_3$	$P'_4$	$Q'_5$		+ $[p_1 + (1-p_1)p_2] p_3 (1-\alpha) P'_4 Q'_5$
00101	$(1-p_1)(1-p_2)$	$p_3$	$Q'_4$	$P'_5$		+ $[p_1 + (1-p_1)p_2] p_3 (1-\alpha) Q'_4 P'_5$
00100	$(1-p_1)(1-p_2)$	$p_3$	$Q'_4$			+ $[p_1 + (1-p_1)p_2] p_3 (1-\alpha) Q'_4$
00011	$(1-p_1)(1-p_2)(1-p_3)$	$p_4$	$P'_5$			+ $[p_1 + (1-p_1)p_2 + (1-p_1)(1-p_2)p_3] p_4 (1-\alpha) P'_5$
00010	$(1-p_1)(1-p_2)(1-p_3)$	$p_4$	$Q'_5$			+ $[p_1 + (1-p_1)p_2 + (1-p_1)(1-p_2)p_3] p_4 (1-\alpha) Q'_5$
00001	$(1-p_1)(1-p_2)(1-p_3)(1-p_4)$	$p_5$				+ $[p_1 + (1-p_1)p_2 + (1-p_1)(1-p_2)p_3 + (1-p_1)(1-p_2)(1-p_3)p_4] p_5 (1-\alpha)$
00000	$(1-p_1)(1-p_2)(1-p_3)(1-p_4)(1-p_5)$					