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POPULATION DYNAMICS OF DUCKS IN
CANADA : THE RATIO OF
IMMATURES TO ADULTS

by

John Stephen Wendt B.Sc. M.Sc.

A thesis submitted to the Faculty of
Graduate Studies and Research in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

A method is described that allows comparison between survival rates determined from bird band recoveries and age ratios obtained from wings of ducks killed by hunters. The method can be used to monitor population change.

To allow interpretation of the age ratios from wings, a comprehensive set of correction methods was used. For example, the ratio of immature mallards to adults in the wings from the prairie region of Canada in 1974 was 2.77. This was corrected for the tendency for young to be killed at a higher rate than adults, to give 0.966. It was corrected to allow for different kill rates of adults and immatures of both sexes, with the result 0.922. A correction for errors of identification, when a wing is assigned to the wrong category of age and sex, gave the result 2.308. Correction for both sources of error, and restriction to females only gave the result 0.757. Variances were calculated for all estimates of age ratio.

Not all of the corrections were found to be justified at all times. The degree to which young are more vulnerable to hunting than adults was found to be important, and variable from year to year, in all species examined. Identification errors for mallards could often be ignored, but for other species such as black duck, they were important.

The methods were adapted for the estimation of sex ratio. The ratio of male to female mallards from prairie Canada was found to be about 1.0 in 1979 and 1980, but 1.5 in 1981, declining to 1.1 in 1982.

The analysis indicated decrease for prairie mallard populations following 1972 and 1980 and increase after 1975 and 1977, although breeding birds displaced north in 1977 because of low water levels that year escaped detection in this study. Black duck populations in the maritimes were relatively stable up to 1982. In Ontario and Quebec, black duck have declined, but this study indicates that excessive hunting is not a main cause. 1972 is indicated as a poor production year for ducks in eastern Canada.

1 - INTRODUCTION

This paper is concerned with changes in population level of ducks in North America. More specifically it deals with populations from a global, rather than a local viewpoint (see Terminology), with emphasis on the estimation of annual productivity of ducks as determined by the ages of ducks killed by hunters.

One view of ducks is as a resource from which we manage to obtain benefits (hunting). An understanding of their population dynamics could direct management strategies to provide for better yield, in the sense of greater, less variable, or more evenly distributed yield. Of deeper significance is the need to monitor the effects of hunting on populations to ensure that exploitation by man does not lead to a risk of extinction for any species.

A more recent impetus for the study of duck populations is the realization that ducks are of potential value in the application and testing of ecological theory. Toft et al. (1982), for example, chose ducks for an investigation of species interactions, because of the large number of closely related species that occur sympatrically in areas that would not be expected to have high point diversity (being of temperate and arctic climate).

The extensive quantity of population data that have been gathered as a guide to the regulation of hunting could be an added advantage to the study of ducks as a taxonomic group. Large areas of the prairie and parkland breeding habitat have been surveyed by airplane since the 1950's to estimate population as well as habitat condition and the production of young. Before that time ground based surveys were used. Surveys of hunters to

estimate kill of waterfowl, the determination of age and sex composition of the kill, and extensive banding programs give unusual records of population characteristics on a global level.

These population data have been used most often for the first purpose mentioned above, the monitoring of an exploited resource. Implicit in this has been a reliance on indices derived from standard methodology.

There are two reasons why the large-scale data gathering programs for ducks have been little used in theoretical ecology. The most obvious is the lack of homogeneity in much of the data (discussed for the case of banding returns in chapters 3 and 4). Simple relationships that may be apparent from one study are subject to testing with many observations widely separated in space and time. This makes a confusing arena for speculation. A second reason for biologists being slow to use continental survey data for purposes other than management is that the results are difficult to validate and interpret. They involve surveys over wide areas with major logistic constraints (some remote areas have very little bird banding, for example), and too much scope for interference from uncontrolled variables (such as habitat and climate variation). Despite these difficulties, the value of this information for management uses comes from the long period of study with fairly constant methods, which should produce useful indices even when the results cannot be interpreted as unbiased estimates of true population sizes, birth rates, or death rates.

There has been a recent growth in the use of large-scale data for testing of theory (e.g. Nudds, 1983). Patterson

(1979) attempted to use aerial survey counts and hunter survey estimates to categorize prairie ducks by ecological strategy, but this was a first attempt that included no validation of the data. It also seems that his use of the r-K framework (MacArthur and Wilson, 1967) may not be sufficiently detailed for classification, as shown from a theoretical point of view by Demetrius (1975, 1981). This topic is considered again in the discussion of this thesis.

The United States Fish and Wildlife Service attempts integration of data from continental banding and surveys, but some recent work (eg. Anderson 1975, Anderson and Burnham, 1976) has primarily served to highlight the need for rigorous analysis and substantial data sets. Martin et al. (1979) review the large-scale methods now in use for the study of duck populations. They built models that combined estimates of parameters from banding and various surveys, to confirm that the parameters were consistent. Munro and Kimball (1982) dealt with the age and sex structure of mallard populations, primarily using banding data, but they also compared distribution of mallard harvest from band recoveries and harvest surveys.

This study is an interpretation of one component of the continental waterfowl surveys, namely, the age ratios of duck populations determined from specimens received from hunters in wing surveys. (The mechanism of wing surveys will be explained in more detail later in this chapter.)

Using age ratios to monitor duck populations

Age ratios have been calculated and published for many populations of ducks (and other wildlife species), but

as Caughley (1974) claimed, "... these are seldom interpreted. One's curiosity over why these data were collected, or what they reveal about the population, is usually left unsatisfied by the author."

Caughley was not optimistic about the usefulness of age ratios. He directs this comment to waterfowl managers: "A wildlife manager, using only age ratios to monitor a population, would come completely unstuck if faced by a massive increase or decrease in numbers brought about through a general change in the rate of survival." He summed up his argument, "age ratios cannot be interpreted without a knowledge of rate of increase, and if we have an estimate of this rate we do not need age ratios."

Caughley's claim that the collection of age ratios is pointless seems reasonable in the light of the published use that has been made of age ratios from duck wing collections. Tables of age ratios from widescale wing collections in Canada, the United States, and Britain have appeared but with no measures of precision. In addition, few corrections have been made for known sources of bias. Finally, the age ratios have been presented alone, in most cases, without reference to other population statistics. However Caughley's argument that the rate of increase must be known to allow interpretation of age ratios is misleading. In particular, Martin et al. (1979) suggest that, for ducks, population size variation is more closely related to changes in reproductive rate than survival.

One component of population change is the production of young. The other is death. A detailed population model requires that the boundaries of the system be specified,

that immigration and emigration be incorporated as birth and death, and that the population be subdivided according to age, sex, or other categories. Still the basic model is the same, that the population change is equal to additions minus depletions. With knowledge of two components, we can calculate the third. While many studies have used the assumption of a stable age distribution to interpret age structure as a means of estimating mortality rates, in this study the age ratio is used as a measure of the birth rate. Mortality is estimated from banding returns to allow development of a population change index.

This study addresses the problem of using age ratios from the Canadian wing collection survey to provide useful information about population status for duck species over wide areas. As might be expected, the results have to be qualified by place and species, and by the quality and quantity of information available both from the wing sample and related results from bird banding.

The most important question is, when do the numbers we get from the survey provide valuable information about the living population's age composition; alternatively, when are errors from sampling and various biases so severe that little of use remains? Furthermore, when age ratios are available, how can they be interpreted biologically, and if they are not now measured properly, could methods be developed to improve estimation?

To answer the first question, sampling errors were estimated, incorporating corrections of known bias in identification of the age classes, and of differences in the likelihood of birds being killed by hunters. Often

for species in particular regions, it was found that either the main sample of wings from hunters or the supplementary information needed for error correction was insufficient for reliable estimation. In other cases the estimation was reasonably good, and it was possible to address more specific questions:

- How can age ratios be used to indicate population status? This was answered by combining age ratios with independent estimates of annual survival.

- How do age ratios compare between similar species in the same region? An example is presented comparing the closely related mallard and black duck. This comparison is especially interesting because it may be that competition between them is causing population changes. The age ratio results are consistent with this hypothesis.

- How do results from the same species compare between two regions? This may show how a species' ecological strategy differs in areas of different habitat type or variability. The mallard is useful for making a comparison between the prairies, where age ratios are low, and Ontario and Quebec, where they are higher. The apparent variation with the prediction by Patterson (1976) that the prairies would have higher production because of better nutritional sources, may be explained in part by man's degradation of prairie breeding habitat.

- How will age ratios be useful in understanding the continental ecology of waterfowl? In effect this study is intended to estimate the realized rate of increase, r , for duck populations. It does this by a widespread,

efficient sampling device, using thousands of volunteer hunters. With better banding samples it should be possible to use age ratios to help understand differences in ecological strategy among species (Patterson, 1979). This study shows, however, that one traditional approach, using theory based on stable age distributions, must be modified.

Several recent field studies of duck populations have attempted to bring the methods of community ecology to the study of waterfowl. Typically, they make use of relatively new multivariate statistical techniques to reduce complex sets of data so that patterns of interest will become evident. Toft et al. (1982) used multiway contingency analysis to search for relationships between species and pond use for breeding ducks, with the main purpose being to look for evidence of competition among species. White and James (1978) used principal component analysis and multivariate analysis of variance to investigate niche separation of wintering waterfowl. Nudds (1983) used discriminant function analysis and principal component analysis to look for niche separation in breeding waterfowl. These multivariate techniques are called into play when the number of variables and interactions becomes too large to be reliably assessed by simpler methods. In the cases cited, useful simplifications were produced, demonstrating differences in habitat use and feeding behavior among species in the study areas.

If these ecological differences, as determined from local studies, have evolutionary significance to a species then they should be reflected as well globally. Thus if competition between two species is apparent in a local study, but on a global scale it turns out that the

population levels of the two species are not related, then the local effect is of little evolutionary significance. This is especially true considering the vagile nature of duck species and the wide area of the northern hemisphere over which they have evolved. Most species in this study now range over most of the northern hemisphere, or have close Eurasian relatives that are not very distant in evolutionary time.

It is necessary that local relationships be corroborated, where possible, on a global scale. To this end, studies such as this one are needed to delineate the applicability of wide scale surveys. The results found here do not satisfy this need on their own, but constitute one step on the way.

Outline of chapters

The first chapter provides a brief history of the use of age ratios by waterfowl biologists, and an introduction to the wing survey carried out in Canada.

The second chapter provides a mathematical framework for the interpretation of age ratios using estimates of survival from bird band recoveries. Here the notion of a critical age ratio is introduced and calculated for several typical data sets.

The third chapter deals with the biological framework for the estimation of age ratios, including techniques of identification, the changes in age ratios during migration, and the environmental changes during the study period.

The fourth chapter develops the mathematical techniques used in this investigation to control for inaccuracies, and estimate sampling error in the determination of age ratios. There are 14 correction models, each with a set of rules for adjusting the number of wings in various categories in the wing sample. These models form the basis for the discussion of results from this study.

The fifth chapter deals with other related topics that are not dealt with in detail in this report. An attempt is made to use estimated age ratios to estimate other population parameters, using the change-in-ratio method (Seber, 1982). Further, it is shown how the methods of this study could be used to estimate sex ratios, with correction for inaccuracies and calculation of sampling errors.

Chapter 6 presents those results that have not appeared earlier in the report. Those results that have been used to illustrate previous discussion are summarized. This chapter is organized by species within regions. The variety of results, which stems from the variety in quality and quantity of data and from the differences among the species, prevents the presentation of results according to a common format for all data sets.

Chapter 7 presents a discussion of the findings of the study, with recommendations. Comparisons are made with other surveys that took place over the same time period. The comparisons of mallard with black duck, and prairie mallard with eastern mallard production are given here. Some recommendations are proffered for future operation and analysis of wing collection surveys, and for putting the work into a broader ecological context.

Chapter 8 summarizes the findings of this study.

Appendices provide those further details of methodology and results that could be removed from the main body of the text without disrupting the presentation.

Terminology

Most terms are explained in the text. A few that are used throughout the thesis are explained here.

Writing of sex ratios in birds, Aldrich (1973) listed four sex ratios that can be considered; primary at fertilization, secondary at hatching, tertiary in immatures, and quaternary in adults. In this spirit we define a primary age ratio as the number of eggs laid per adult, a secondary age ratio as the number of young

hatched per adult, and a tertiary age ratio as the number of immatures fledged per adult.

In this report the basic definition of age ratio is the third, the number of young fledged per adult. This study does not address the loss of eggs, or of young that have not fledged.

In the population model the period of time between hatching and fledging is compressed to an instant. Thus the time from about May until the start of the hunting season is considered an instantaneous event leading to the production of fledged young. This is termed the periodic breeding event. From this it follows that the time when adults are counted relative to this breeding event is the time of hatch. The young, however, are counted just before the start of the hunting season. A working definition is to define the age ratio to be estimated in mid-August.

Following this usage, the term immature is used for those individuals that are less than one year old during the hunting season. At this time most immature birds are from 2 to 8 months old.

The word population is used in the statistical sense to mean the group of objects about which inferences are to be made on the basis of sampling. No genetic connotation is implied. The common usage as "the total number of animals" is used, as well.

The term "ecological strategy" is purposefully vague. It is used to indicate the set of variables of natural history that make up the way of life of a species. It is implied that these variables have been subjected to natural selection, and in this way form a strategy for

survival. Here reproductive output, age of first breeding, migratory patterns, feeding behavior, and interspecific aggression are examples of phenomena that are included.

The distinction between a local and a global approach is also vague. Duck species are highly migratory and wide ranging. A global approach is one of a broad enough geographical coverage that most of the breeding, migratory, or wintering range of a population (here in a genetic sense) is included. A global investigation covers the area that is available to individual birds in their choice of places to live.

Notation

Throughout this paper R represents the ratio I / A , variously subscripted, where I and A are the number of immatures and adults, respectively. R is used because of its relation to average brood size, instead of the alternative,

$$P = I / (I + A)$$

that is sometimes preferred because of its mathematical tractability. If the proportion of immatures in the total population is P then the following relations hold:

$$P = R / (1 + R) \quad \text{and} \quad R = P / (1 - P). \quad (1)$$

If R , I , and A are considered as functions of time, and time is measured from a fixed time of hatching, then, with simplifying assumptions of synchrony among the population, and homogeneity among individuals, we can develop models of the population growth and structure.

The age ratio is one parameter of particular interest.

Field identification of ducks is usually limited to categorizations of bird-of-the-year, non-breeding, and breeding. More detailed models, that allow for complete categorization by age, are of theoretical interest, but bring additional difficulties in the estimation of parameters, especially when field data can not be obtained for the older age classes. For this reason it is beneficial to develop a notation that ties the general case to the adult/immature grouping of individuals.

The full population, N , is divided into subsets, denoted N_x , where the subsets may be determined by age in generations, age in years, age as adult/immature, combinations of age and sex, or otherwise. The subscript is chosen appropriately:

N_0 : the number of individuals between birth and 1 year (or generation) of age.

N_I : the number of individuals in category "immature".

N_{AF} : the number of individuals in category "adult female".

Populations are changing according to continuous processes so it is sometimes necessary to express N_x as a function of time, $N_x(t)$. This notation is used in the development of some formulae but will not be retained in models using survey data where that data will be combined for the whole hunting season or, for some analysis, the month of September.

It is often convenient to drop the N and refer to the number of individuals in a group by the group identifier, thus I and A to refer to N_I and N_A .

A similar notation is used for survival, where survival of immatures is denoted S_I and survival of adults as S_A .

History of the use of duck age ratios

The age ratio has been recognized as an important statistic of duck populations. With the sex ratio (which is closely associated in interpretation with the age ratio) age ratios have been collected and used to characterize population status since 1930, at least. Bellrose et al. (1961) give a brief review of the early history of age ratio study in wild duck biology. They quote Leopold writing in 1933, "All measurements of either game population or game productivity are enhanced in their significance and value if the sex and age as well as the number of individuals be determined". This original concern for age and sex identification stems in part from a recognition that life history parameters are different among the age and sex classes. Anderson (1975) tested the hypotheses that survival and band recovery rates differed among age and sex classes of mallards. He determined that the rates for adult males and females differed, and that those for adults differed from those for young. The extent of the differences was large enough to invalidate the pooling of age and sex classes indiscriminantly in any population analysis of mallards. This underlines a basic concern for the age ratio as a characteristic of duck populations.

Another early worker showing concern for the measurement of the relative size of age and sex classes was Lincoln (1932), in his appealingly titled paper, "Do drakes outnumber susies?". His demonstration that adult male ducks outnumber adult females led to a concern that hunting practices were creating an imbalance in duck population structure. Part of the reason that early studies relating to ratios between components of duck populations paid most attention to sex as opposed to age stems from the lack of knowledge by field workers of

methods that were available for distinguishing immature ducks from adults. During the hunting season, when large samples of birds are available for examination in the hand as well as observable in the field, the plumage of young and adults of many duck species is usually not easy to discriminate. For most of the year, however, the plumage differences between the sexes are great enough that adults of all Canadian species except the Black Duck can be distinguished in the field. Birds in the hand can usually be identified as to sex by characteristics of plumage and bill markings. Studies based on sex could be carried out without killing and dissecting the specimen, with methodology that was available to early waterfowl biologists.

In North America the development and field use of reliable aging techniques followed a paper by H. A. Hochbaum (1942) which explains the difference in cloacal structure among the four categories of age and sex that are of concern in this study. Larson and Taber (1980) describe the utility of cloacal age/sex determination, which is summarized here:

Presence/absence of penis - reliable distinction between male and female (if the cloacal inversion is properly accomplished).

Penis size/appearance - reliable distinction between adult and young males for
 mallard, pintail, black duck(probably)
 until mid-November
 gadwall, American wigeon, shoveller,
 green-winged teal, blue-winged teal,
 redhead, canvasback, lesser scaup
 until end of year.

Presence of a large bursa of Fabricius - generally acceptable during the hunting season as a proof of immaturity in species that breed at one year of age.

The condition of the oviduct opening is of significance in females, as well. The reliability of cloacal determination of age and sex is not absolute. Larson and Taber point out the difficulty in seeing the characteristics in a live female duck, and recommend that the cloaca be relaxed by swabbing with a solution of cocaine. This technique is probably advantageous, but is not widely used. The data in this paper that are based on cloacal determinations of age and sex have not had the benefit of such a detailed approach. There is opportunity for error in any cloacal examination, inexperienced banders often have difficulty everting the cloaca, and sometimes fail to find a penis that is present, or confuse the penis with the much smaller clitoris in the female.

The use of better methods of identification in the field allowed the Illinois Natural History Survey to carry out long term studies of sex and age ratios, starting with the work of Arthur S. Hawkins in 1938. Bellrose et al. (1961) report the results of this investigation. They made the point that the age ratio and sex ratio are linked. Because the sex ratio starts near (1:1) in immature ducks, and then (in general) diverges to favor males in later age classes, it follows that the greater the proportion of older birds, the greater will be the proportion of males. In this way Bellrose et al. related sex ratios to the production of young in specific years (i.e., if the ratio of males to females dropped, they inferred a good production of young). Bellrose (in

Hanson and Smith, 1950) initiated the correction of age ratio data for the relative vulnerability to hunting of the two age categories, estimating the relative vulnerability as the ratio of recovery rates from banding data. He also discussed the variability of age ratios among places, at different times, and with different sampling techniques. He used age ratio estimates as indices of production.

In 1958 the government organization, now known as the U.S. Fish and Wildlife Service, began collecting wings from ducks killed by hunters to allow the determination of the species, age and sex composition of ducks being killed. This opened the opportunity for monitoring waterfowl populations in North America on a scale never before attempted. By 1961 all areas in the United States were included in the survey. The identification of species from wings presented few problems, but to include age and sex information required the development of new keys for the discrimination of the various groups. S.M. Carney and A.D. Geis (1960) described the first of the keys produced for the survey, in this case for the mallard. This was followed by publication of the keys now in use in the survey (Carney 1964). Since 1961 the results of the United States surveys have appeared in various publications, notably the U.S. Fish and Wildlife Service Waterfowl Status Reports, which appear approximately yearly.

The possibility of a wide, uniform collection of valuable statistics from wings has appealed to workers in other countries, as well. Wing collection surveys were started in Britain in 1965, in Finland in 1967, in Sweden in 1967, and in the U.S.S.R. in 1969. Boyd Harrison and Allison (1975) give a key to the

identification of British duck wings, with some examples of analysis from the British surveys. Boyd Cooch and Harrison (1976) give further examples of analysis. Both papers use age ratios as indicators of the yearly production of young.

In 1967 the Canadian government started a similar mail survey of hunters to determine the composition of the annual kill of ducks. This report describes a study of the results from that survey for the period 1971 through 1982, during which 274,391 duck wings were received. The methodology of this survey is described in Cooch et al. (1978).

A goal of the duck wing survey is to estimate the number of birds of each species killed. This requires that wing data be combined with questionnaire data from the Canadian migratory game bird harvest survey. Results from this combined analysis are presented for some species in chapter 7.

2 THE INTERPRETATION OF AGE RATIOS

The Interpretation of wing survey results

An observed distribution of wings by age and sex classes can have many interpretations which should be systematically considered according to their implied importance. Some are described below.

1. The age composition reflects the annual production of young. Non-production by non-breeding adults is incorporated in the overall age ratio.
2. The age composition reflects the makeup of the population in the region of study before the start of the hunting season. It may therefore include a disproportionate number of some age or sex class when the pre-season dispersion and migration are heterogeneous.
3. The sex composition in the young reflects the tertiary sex ratio in the population, which is generally thought to be approximately 1. (The tertiary sex ratio is the ratio of males to females at the time when young birds fledge.)
4. The sex composition in adults reflects the continuing change in ratio that results from differential mortality of males and females. (for example, a greater chance of death for females will lead to an increased relative number of males).
5. The true composition in the population is not represented accurately in the wing sample because the classes differ in vulnerability to hunting and so are reported at different rates. (If young are

more likely to be killed by hunters than are adults, the wing sample will contain a disproportionate number of young bird wings.)

6. The identification of wings at wing bees has errors that distort the apparent composition of the sample.
7. The sample differs in composition from the population because of chance.
8. The sample does not represent a homogeneous population in time.
9. The hunter may not send a representative sample of his kill.
10. Because the survey is based on a selection of hunters and not wings a low within-hunter variance may allow a false impression of precision.
11. Errors may be made in the processing of survey material, the coding of results, and the computation of estimates.

The central theme in this study is to control for as many of the above factors as possible, leaving (1), the annual production of young, as the primary explanation of the changes in age ratio that remain after correction of the data. The resulting index can then be compared with estimates of survival to indicate change in population levels.

The correction methods used are described in Chapter 4. At the end of that chapter the extraneous sources of error (2, and 5-11, above) are reviewed.

The significance of age ratios in duck population dynamics

The ratio of immatures to adults is of interest in the population dynamics of any species. Consider a model of a population in which only birth and death are causing population changes, and in which the following relations hold:

$$N_I(t) = N_A(t) b, \quad t = 0, 1, 2, 3, \dots \quad (2)$$

(that is, the number of individuals at the start of a generation is equal to b , the mean recruitment rate of fledged young, times the number of adults alive at that time.)

$$N_A(t) = N_A(t-e) + N_I(t-e), \quad t = 1, 2, 3, \dots$$

(that is, the number of adults in the succeeding generation is equal to the total of immatures surviving from the previous year plus all adults alive a short time before the birth event.)

$$\begin{aligned} N_I(t) &= N_I(\text{int}(t)) \exp(-d_I(t - \text{int}(t))) \\ &\quad , t \text{ not an integer} \\ N_A(t) &= N_A(\text{int}(t)) \exp(-d_A(t - \text{int}(t))) \\ &\quad , t \text{ not an integer} \end{aligned}$$

(that is, the number of individuals in each age class declines through the period between breeding events according to an exponential law:

$$\frac{dN}{dt} = -d \cdot N \quad (d > 0.)$$

where the function $\text{int}(\)$ is the integer part, the function $\exp(\)$ is the exponential, and e is a small number used here to represent the instant before the periodical birth event.

Under this model the age ratio has the following form:

$$R(t) = \frac{N_I(t)}{N_A(t)} = b \quad t = 0, 1, 2, 3, \dots \quad (3)$$

$$R(t) = \frac{N_I(\text{int}(t)) \exp(-d_I \cdot (t - \text{int}(t)))}{N_A(\text{int}(t)) \exp(-d_A \cdot (t - \text{int}(t)))}$$

$$= b \exp((d_A - d_I)(t - \text{int}(t))), \quad t \text{ not an integer.}$$

Since immatures usually have higher mortality rates than adults, $R(t)$ decreases between births.

Now compare the number of adults at two breeding times, using the notation $N_I(t) = I(t)$, $N_A(t) = A(t)$:

$$\frac{A(t+1)}{A(t)} = \frac{I(t) \cdot \exp(-d_I) + A(t) \cdot \exp(-d_A)}{A(t)} \quad (4)$$

$$= b \cdot \exp(-d_I) + \exp(-d_A).$$

If the population is to increase, this ratio must be greater than 1:

$$b \cdot \exp(-d_I) + \exp(-d_A) > 1 \quad (5)$$

This can be expressed in terms of the age ratio that was applicable just before the breeding (at time $t-e$):

$$R(t-e) > \exp(d_A) - 1. \quad (6)$$

(condition for increase)

Even without the derivation of this expression (completed below), the interpretation is quite simple in that the right hand side of the equation gives the ratio of losses to survivals in adults. To see this note that the proportion of adults that have died through one time period is given by $1 - \exp(-d_A)$, while the proportion of survivors is $\exp(-d_A)$. Division of these two expressions gives the right hand side of equation 6.

Returning to the derivation of the expression for equation 6, equation 3 is used to give the value of R at time $t-e$, (taken to represent the instant before the breeding event).

$$\begin{aligned} R(t-e) &= b \exp((d_A - d_I) \cdot (t - e - (t-1))) \quad (7) \\ &= b \exp((d_A - d_I) \cdot (1-e)) \\ &= b \exp(d_A - d_I), \text{ in the limit of small } e. \end{aligned}$$

This allows replacement of $(b \exp(-d_I))$ in equation 5 by $R(t-e) \exp(-d_A)$, and equation 6 follows.

For populations that conform to this model we could use an estimate of R taken late in the hunting season, together with an estimate of adult mortality to determine the direction of population change.

Although the population model given here is not detailed enough to simulate all aspects of a wild duck population, it does serve to highlight the importance of the age ratio as a parameter of the system. If adult and immature mortality were equal (which is not ordinarily the case for many species) then R would be constant, and an estimate of R at any point in time would estimate the birth (or hatch) rate.

Relationship of the age ratio to survival rates

In the preceding simple population model equation 6 imposes a condition on the value of R at the end of one generation if the population is to increase.

$$R_{(final)} \geq \exp(d_A) - 1.$$

If S_A is the proportion of adults that survive and M_A is the proportion that do not then, under the assumptions of the model, the criterion can be rewritten according to equation 6a:

$$R_{(final)} \geq M_A / S_A. \quad (6a)$$

We do not have enough wings from late in the season, or banding data from that time of the year, to estimate the final age ratio with much confidence. However if we know the survival rate of immatures, S_I , the final age ratio can be estimated as:

$$R_{(final)} = R_{(fledged)} \left(\frac{S_I}{S_A} \right).$$

The maintenance criterion can then be made in terms of the age ratio estimated from the wing bee:

$$R \geq (1 - S_A) / S_I. \quad (8)$$

This value is called the critical value for R and is denoted R (critical).

If the survival rate of young is not known then we can estimate R (final) by R (fledged). In the context of the model that assumption is equivalent to the assumption that relative vulnerability to all sources of mortality is 1, or that $S_A = S_I = S$.

$$R \geq (1 - S) / S. \quad (8a)$$

Species that do not regularly breed at one year of age would not fit the model used to derive the critical value of R . Survival rates vary by year so the critical value for R will vary also.

Estimates of survival and R (critical)

A major upset for the traditional methods of survival estimation came with the widespread use of maximum-likelihood estimation applied to bird-banding models as discussed, for example, by Seber (1982). The proponents of this approach had few kind words about previous methods, the most usual of which was the life table method. Brownie et al. (1978) are typical, "... the practice of life table analysis should be discontinued. Much better methods (for band recovery analysis) now exist and should be used."

Lakhani and Newton (1983) emphasize the need for additional information to corroborate survival estimates from even the best available estimation techniques. The production data from wing surveys used here provide this sort of corroboration. The age ratios calculated in this study can be compared with the critical age ratio calculated from survival estimates. As will be shown in this report, older published values for survival rates for adults and young give values of R (critical) that are not consistent with the levels of R estimated from the wing samples. The newer methods of survival analysis do give values of R (critical) that are much closer to the values of R estimated. In this way the comparison of age ratio results with survival rates is useful in evaluating the relative bias of survival estimation techniques.

Table 1 draws on Bellrose (1978) who in turn refers to other authors not specifically cited here, reporting the estimates of survival that were available before the work of Brownie et al. (1978).

Table 1. Estimates of $\hat{R}$ (critical) from older techniques

Species	SA	SI	$\hat{R}$ (critical)	Comments
Wood Duck	.48	.40	1.3	Bellrose (1978)
Gadwall	.48	.33	1.6	Bellrose (1978)
G.-w. Teal	.415	.372	1.6	Bellrose (1978)
Mallard	.44	.29	1.9	Bellrose (1978), for Minnesota
Black Duck	.50	.35	1.4	Bellrose (1978), for females
N. Pintail	.57	.34	1.3	Bellrose (1978), AM in Sask I in Man.
B.-w. Teal	.47	.28	1.9	Bellrose (1978), for prairies, using AF for S
N. Shoveler	.39	.29	2.1	Bellrose ^A (1978), small sample
Canvasback	.48	.23	2.3	Bellrose (1978), Sask. 1953-57
Redhead	.45	.20	2.7	Bellrose (1978), Man. 1953
R.-n. Duck	.46	.23	2.3	Bellrose (1978), mixed data set
L. Scaup	.58	.31	1.4	Bellrose (1978),

Unfortunately, most of the older survival estimates were published without estimates of standard error.

Survival rate estimates using the newer methods for ducks banded in the regions of study used in this paper, are not available in published form, and had to be computed. The programs Brownie and Estimate that are described in Brownie et al. (1978) were used. These programs attempt to use a given set of band recovery data to estimate parameters for a series of models with varying assumptions. Chi-squares are calculated to test the fit of the observed data to the expected values from the models with estimated parameters. These, and between-model likelihood tests aid in the selection of a model. The models with more parameters give less extreme chi-square values, but this may reflect nothing more than the flexibility of the more complex models in matching datasets, irrespective of an interrelationship. It is best to select that model in a hierarchy with fewest parameters that has an acceptable test value.

Two advantages in the calculation of survival rates expressly for this study were the matching of geographical regions with the age ratio regions, and the ability to produce estimates of age-specific survival.

The programs used for estimating survival rate calculate standard errors of $\hat{S}_I$ and $\hat{S}_A$, but not of the critical value of R:

$$\hat{R}_{\text{critical}} = (1 - \hat{S}_A) / \hat{S}_I \quad (\text{from equation 8})$$

From equation (6.8) in Cochran (1977), an estimate of the coefficient of variation of R_{critical} can be made:

$$(\hat{cv})^2 = (\hat{C}_{yy} / n + \hat{C}_{xx} / n - 2 \hat{C}_{yx} / n). \quad (9)$$

in which the finite population correction has been ignored, and in which the numerator $y = 1 - S_A$ and the denominator $x = S_I$.

In terms of statistics prepared by the programs,

$$\hat{C}_{yy}/n = \hat{\text{var}}(\overline{S_A}) / (\overline{1-S_A})^2$$

$$\hat{C}_{xx}/n = \hat{\text{var}}(\overline{S_I}) / \overline{S_I}^2 \quad \text{and}$$

$$\hat{C}_{yx}/n = \hat{\text{cov}}(\overline{(1-S_A)}, \overline{S_I})$$

$$\frac{\overline{(1-S_A)} \cdot \overline{(S_I)}}{}$$

$$= - \frac{\hat{\text{cov}}(\overline{S_A}, \overline{S_I})}{}$$

$$\overline{(1-S_A)} \cdot \overline{(S_I)}$$

Thus

$$\begin{aligned} \hat{(cv)}^2 \text{ of } \hat{R}_{\text{critical}} &= \frac{\hat{\text{var}}(\overline{S_A})}{(\overline{1-S_A})^2} + \frac{\hat{\text{var}}(\overline{S_I})}{\overline{S_I}^2} + 2 \frac{\hat{\text{cov}}(\overline{S_A}, \overline{S_I})}{\overline{(1-S_A)} \cdot \overline{(S_I)}} \quad (10) \end{aligned}$$

This formula was used to calculate the standard error of $\hat{R}_{\text{critical}}$, which appears with survival rate estimates in Table 2.

Table 2. Survival rates of Canadian-banded ducks with R
(critical) estimated by maximum-likelihood models

Species	Year	$S_A \pm s.e.$	$S_I \pm s.e.$	$cov(S_A, S_I)$	$R_{critical} \pm s.e.$
wood duck, Ont. & Que.	*	.522 $\pm$.015	.356 $\pm$.025	.00002	1.3 $\pm$.1
	1971	.558 $\pm$.123	.407 $\pm$.070	.00253	1.1 $\pm$.4
	1972	.475 $\pm$.089	.231 $\pm$.052	.00192	2.3 $\pm$.8
	1973	.579 $\pm$.126	.332 $\pm$.074	.00442	1.3 $\pm$.6
	1974	.542 $\pm$.119	.321 $\pm$.071	.00316	1.4 $\pm$.6
	1975	.551 $\pm$.127	.517 $\pm$.125	.00858	0.9 $\pm$.4
	1976	.557 $\pm$.129	.602 $\pm$.121	.00587	0.7 $\pm$.3
	1977	.430 $\pm$.091	.307 $\pm$.065	.00272	1.9 $\pm$.6
	1978	.464 $\pm$.114	.331 $\pm$.087	.00499	1.6 $\pm$.7
	1979	.588 $\pm$.166	.299 $\pm$.082	.00705	1.4 $\pm$.8
green-winged teal	1980	.439 $\pm$.170	.411 $\pm$.152	.01702	1.4 $\pm$.8
	1971	.381 $\pm$.098	.443 $\pm$.079	.00250	1.4 $\pm$.4
	1972	.309 $\pm$.060	.313 $\pm$.055	.00150	2.2 $\pm$.5
	1973	.651 $\pm$.139	.330 $\pm$.075	.00550	1.1 $\pm$.6

Table 2. Survival rates of Canadian-banded ducks with
 (contd.) R (critical) estimated by maximum-likelihood models

Species	Year	$S_A \pm s.e.$	$S_I \pm s.e.$	$cov(S_A, S_I)$	$R_{critical} \pm s.e.$
	1974	.534 $\pm$.124	.455 $\pm$.087	.00560	1.0 $\pm$.4
	1975	.754 $\pm$.157	.587 $\pm$.106	.00720	0.4 $\pm$.3
	1976	.407 $\pm$.070	.333 $\pm$.052	.00120	1.8 $\pm$.4
	1977	.649 $\pm$.114	.498 $\pm$.086	.00630	0.7 $\pm$.3
	1978	.452 $\pm$.086	.346 $\pm$.059	.00200	1.6 $\pm$.4
	1979	.481 $\pm$.106	.402 $\pm$.090	.00610	1.3 $\pm$.5
	1980	.513 $\pm$.149	.412 $\pm$.128	.00960	1.2 $\pm$.6
gadwall	*	.564 $\pm$.058	.350 $\pm$.068	.00390	1.2 $\pm$.4
black duck, maritimes	1971	.631 $\pm$.135	.573 $\pm$.088	.00590	0.6 $\pm$.3
	1972	.542 $\pm$.107	.466 $\pm$.081	.00500	1.0 $\pm$.4
	1973	.435 $\pm$.086	.399 $\pm$.061	.00300	1.4 $\pm$.4
	1974	.587 $\pm$.127	.363 $\pm$.070	.00600	1.1 $\pm$.5
	1975	.764 $\pm$.155	.418 $\pm$.065	.00360	0.6 $\pm$.4
	1976	.599 $\pm$.081	.298 $\pm$.048	.00080	1.3 $\pm$.4
	1977	.551 $\pm$.056	.426 $\pm$.052	.00100	1.1 $\pm$.2

Table 2. Survival rates of Canadian-banded ducks with
 (contd.) R (critical) estimated by maximum-likelihood models

Species	Year	$S_A \pm s.e.$	$S_I \pm s.e.$	$cov(S_A, S_I)$	$R_{critical} \pm s.e.$
	1978	.580 $\pm$.061	.418 $\pm$.053	.00130	1.0 $\pm$.2
	1979	.739 $\pm$.083	.643 $\pm$.078	.00290	0.4 $\pm$.2
	1980	.652 $\pm$.117	.608 $\pm$.117	.00920	0.6 $\pm$.3
black duck, Ont. & Que.	*	.618 $\pm$.022	.564 $\pm$.041	.01260	0.7 $\pm$.2
pintail	1971	.590 $\pm$.072	.577 $\pm$.067	.00230	0.7 $\pm$.2
	1972	.670 $\pm$.077	.605 $\pm$.078	.00210	0.5 $\pm$.2
	1973	.798 $\pm$.095	.512 $\pm$.087	.00340	0.4 $\pm$.2
	1974	.681 $\pm$.080	.552 $\pm$.052	.00180	0.6 $\pm$.2
	1975	.688 $\pm$.068	.621 $\pm$.062	.00180	0.5 $\pm$.1
	1976	.672 $\pm$.060	.625 $\pm$.055	.00120	0.5 $\pm$.1
	1977	.748 $\pm$.081	.811 $\pm$.101	.00510	0.3 $\pm$.1
	1978	.625 $\pm$.077	.568 $\pm$.068	.00220	0.7 $\pm$.2
	1979	.653 $\pm$.088	.601 $\pm$.078	.00440	0.6 $\pm$.2
	1980	.874 $\pm$.149	.998 $\pm$.176	.01440	0.1 $\pm$.2

Table 2. Survival rates of Canadian-banded ducks with
 (contd.) R (critical) estimated by maximum-likelihood models

Species	Year	$S_A \pm s.e.$	$S_I \pm s.e.$	$cov(S_A, S_I)$	$R_{critical} \pm s.e.$
mallard, Que. & Ont.	*	.605 $\pm$.009	.576 $\pm$.020	.00320	0.7 $\pm$.1
mallard, prairies	1971	.643 $\pm$.029	.452 $\pm$.024	.00018	0.8 $\pm$.1
	1972	.600 $\pm$.026	.423 $\pm$.024	.00026	0.9 $\pm$.1
	1973	.637 $\pm$.031	.557 $\pm$.036	.00038	0.7 $\pm$.1
	1974	.730 $\pm$.032	.470 $\pm$.023	.00022	0.6 $\pm$.1
	1975	.735 $\pm$.025	.608 $\pm$.026	.00018	0.4 $\pm$.1
	1976	.623 $\pm$.018	.470 $\pm$.019	.00009	0.8 $\pm$.1
	1977	.715 $\pm$.022	.534 $\pm$.028	.00021	0.5 $\pm$.1
	1978	.688 $\pm$.021	.521 $\pm$.023	.00013	0.6 $\pm$.1
	1979	.698 $\pm$.022	.605 $\pm$.028	.00022	0.5 $\pm$.1
	1980	.553 $\pm$.019	.484 $\pm$.030	.00014	0.9 $\pm$.1
blue-winged teal	1971	.468 $\pm$.064	.422 $\pm$.043	.00100	1.3 $\pm$.2
	1972	.632 $\pm$.072	.479 $\pm$.053	.00190	0.8 $\pm$.2
	1973	.662 $\pm$.084	.595 $\pm$.074	.00340	0.6 $\pm$.2

Table 2. Survival rates of Canadian-banded ducks with
 (contd.) R (critical) estimated by maximum-likelihood models

Species	Year	$S_A \pm s.e.$	$S_I \pm s.e.$	$cov(S_A, S_I)$	$R_{critical} \pm s.e.$
	1974	.597 $\pm$.075	.462 $\pm$.047	.00170	0.9 $\pm$.2
	1975	.649 $\pm$.074	.569 $\pm$.058	.00220	0.6 $\pm$.2
	1976	.587 $\pm$.059	.504 $\pm$.047	.00100	0.8 $\pm$.2
	1977	.623 $\pm$.063	.457 $\pm$.058	.00180	0.8 $\pm$.2
	1978	.709 $\pm$.077	.603 $\pm$.060	.00190	0.5 $\pm$.2
	1979	.594 $\pm$.061	.553 $\pm$.064	.00150	0.7 $\pm$.2
	1980	.529 $\pm$.059	.348 $\pm$.063	.00110	1.4 $\pm$.3
redhead	*	.631 $\pm$.021	.312 $\pm$.033	-.00004	1.2 $\pm$.1
lesser scaup	*	.594 $\pm$.040	.476 $\pm$.096	.00011	0.9 $\pm$.2
wigeon	*	.545 $\pm$.024	.575 $\pm$.067	.00011	0.8 $\pm$.1
common eider	*	.663 $\pm$.070	.663 $\pm$.070	.00000	0.5 $\pm$.1

* all years combined - see choice of models in Appendix 1.

Identification methods

To assess the effect of methodology on the results obtained in the survey, it is important to review the techniques used to divide wings among the age and sex classes. In many species the possibility of error in classification is greater for some groups than others. For example, in the classification of dabbling duck wings more errors are made in identifying adult wings than immature wings.

Wings are classified according to differences in colour, size, and texture of particular feathers and feather groups. The criteria used vary among species. Some background on the naming of feathers and the timing of feather replacement (moult) is necessary.

The wing of a duck is illustrated in figure 1 (from Palmer 1962). The primaries are associated with the manus. Most ducks have 10 primaries in evidence, although there are 11 in the strict sense. The secondaries are associated with the ulna, and the tertials are associated with the humerus. The latter groups are not as clearly differentiated as the primaries are from the secondaries, although in ducks the size and shape of the tertials mark them as distinct from the secondaries. Most ducks have 10 secondaries, although the count varies among species. Coverts are feathers that serve to smooth the contour of the wing and body and are identified as in the figure.

Figure 1. The Wing of a Duck (from Palmer, 1962)

Boyd et al. (1975) described the postjuvenile moult of dabbling ducks:

Primaries	No moult
Secondaries	No moult
Tertials	Moulted
Primary coverts	No moult
Greater coverts	No moult
Greater tertial	
coverts	Moulted
Post humerals	Moulted
Scapulars	Moulted
Middle and lesser	
coverts	No moult

That the moult of tertials is underway during the hunting season is of particular significance because the tertials are more or less distinctive in the young of many species. If a wing has a tertial that is clearly juvenile, this is evidence of the bird's age. The lack of a juvenile tertial does not imply that the bird is adult, however, because of the continuing moult. The moult generally proceeds from the tertials to the greater tertial coverts, thus the identifier must look to the coverts when the tertials themselves are inconclusive. Unfortunately the criteria for identification are of variable certainty and the search for a juvenile feather may lead to a decision on the basis of less information than is desirable. The result is a certain tendency for "difficult" wings (those with excessive wear, or with feathers of shape or colour that are intermediate between the obvious types) to be classified as juvenile on the basis of only a feather or two. The opposing error, of calling a juvenile in advanced moult an adult must also occur, but in the Canadian wing samples this error seems to be less

frequent in the species for which we have examined the identification of known material.

Not all of the feathers are present on every sample received. In particular the scapulars (which can be very useful in identification) are often missing. Less frequently the hunter leaves behind some or all of the tertial feathers when he cuts the wing away from the body. On some wings the tips of the primaries are cut, making measurements impossible. Some wings are cut at the wrist joint and include only the primaries and primary coverts. Finally dirt, scorching, wax, or the effects of putrefaction can obscure details of feathers that are present. The combination of these factors means that the sequence through the key differs depending on the condition of individual wings.

Boyd (1970) dealt with the sources of error inherent in wing identification. He gave a summary, adapted slightly in Table 3.

Because a part of the wing sample lacks feathers that are important to the identification Boyd stressed the need for alternate methods of identification. He commented as follows.

1. Because the tertials and tertial coverts are often missing it is necessary to use criteria based on more distal areas of the wing. Boyd suggested that the identification of Canadian wings samples should start with the distal area of the wing.

2. The reliability of wing identification is not much increased by the consideration of many rather than few characters.

3. The presence of one or a few juvenile feathers does not necessarily imply that the bird is immature as it is not uncommon for feathers to be retained during a moult.

4. Age ratios are particularly sensitive to errors in identification of adults, because of the large proportion of immatures in most samples.

5. Canadian wing samples, being taken early in the year, should have fewer cases of immatures being called adults because of advanced moult, and more cases of adults being called immatures because of incomplete moult than the sample taken later in the United States.

Table 3. Sources of error in wing identification

Biological Sources	Size of bird and wing	
	Size and form of feathers	
	Timing and completeness of moult	
Handling	Hunter	Completeness of specimen
		Fouling
		Freshness
		Completeness of questionnaire
	Post Office	Freshness
	Biologist	Additional handling damage
		Match of wings to correct questionnaire
		Recording errors
Inspection	Choice and definition of characters in response to wing condition	
	Accuracy of recognition of characters	
	Reliability of characters for identification	

Identification must be done in such a way that it does not distort the age ratios. For example, light edging on the inner webs of distal primary coverts is considered a reliable characteristic of immaturity in mallards. The lack of this characteristic does not imply adulthood however, as some immature birds have no marked edging. If this criterion were used alone all adult birds would be classed as unknown age, together with some immature birds. Such an approach would provide no useful information about the age ratio. In practice the primary coverts of mallards are used to identify some young birds, but this is supplemented with positive criteria for the identification of adults.

The process of identification takes place at wing bees (named in analogy to quilting bees) at which experienced biologists assemble to process all of one hunting season's wings. They use systematic rules for identification, called keys, that are specific to each species to identify each wing.

/ A summary of rules used for identification of duck wings is given in Appendix 2.

Variation of age ratios during the hunting season

One important aspect of heterogeneity in the age ratios from wings received is the change in this ratio during the sampling period. In the ideal situation discussed in the introduction we might assume a constant relative vulnerability between adults and immatures. If the relative vulnerability is greater than 1 then immatures would be removed from the population at a faster rate than adults and we would expect the age ratio to drop

throughout the season. In real life the situation is much more complicated. The relative vulnerability will be shown to vary during the hunting season, for while hunting is going on there may be continuous immigration and emigration that involves some of the age / sex classes more than others. Perhaps the most evident finding from examination of wings as they vary through time is the irregularity in ratios calculated from small samples. Late in the season samples become very small, both because hunting activity decreases and also because the participation in the survey by hunters declines. Even when data are pooled for several years there are usually not enough wings received to produce consistent patterns in the late season age ratios.

To illustrate the pattern in age ratios from wings received during a season, wing data from the 12 years 1971 to 1982 had to be pooled. The plots of these data day by day were rather erratic in appearance so 3-day running averages were used to smooth the graphs.

Figure 2 is characteristic of many of the patterns found. This shows the age ratios during the hunting season in the prairie provinces, with all dabbling ducks (except Northern Shoveler and Blue-winged Teal, which have unusual patterns associated with early migratory movement) combined. The peak at the start of the graph represents a short time when immatures are much more vulnerable or more abundant than adults, around the opening of the season. The wing age ratio decreases for a while possibly due to removal of young at a greater rate than adults (but not with the original difference in vulnerability). Later the age ratio increases, possibly because of the entry into the heavily hunted areas of new groups of ducks that may have higher ratios

of young. It may also be that the incoming birds have had less exposure to hunting and so have higher relative vulnerability between immatures and adults.

The graph in figure 3 seems much less tractable. This represents the changing age ratio in receipts of Black Duck wings from Eastern Canada. The graph has two pronounced peaks at the beginning instead of one. The reason for this is the combination of different opening dates for hunting, giving two major time periods when, on the average, numbers of immatures were having their first exposure to hunting. The graph is erratic due in part to smaller samples by date for Black Ducks than were available by pooling species. The pronounced and drawn out period of higher age ratios late in the season could well represent a sustained immigration of groups of Black Ducks that have suffered little hunting in northern areas.

If wide areas of Canada are combined the graphs of wing age ratios by date are simplified for several reasons. One is that there are many different opening dates for hunting across the country, so that the peaks from individual regions tend to combine smoothly. By including large areas local effects of immigrant birds are reduced. The variation in results is also reduced by larger sample sizes. Figure 4 shows the pattern of age ratios in wing samples for all the dabbling ducks (except Northern Shoveler and Blue-winged Teal), pooled for all of Canada. With the local contributions reduced by pooling, the impression is of a sustained drop in the age ratio due to differential removal of young.

Figure 5 shows a similar functional form for age ratios from all ducks in British Columbia. British Columbia is

the most isolated region in Canada with the most localised duck breeding habitat. The effects of immigration are therefore less pronounced there so that the change in age ratios is best explained by preferential removal of young (by hunting and non-hunting mortality) from a relatively closed population.

In chapter 5 an attempt is made to use changing age ratios to measure other population parameters, with little success.

Figure 2. Pattern of Age Ratios in Prairie Provinces for all Dabbling Ducks except Northern Shoveler and Blue-winged Teal.

Figure 3. Pattern of Age Ratios
in Eastern Canada
for Black Duck.

Figure 4. Pattern of Age Ratios in
all provinces for all Debbling
Ducks except Northern Shoveler
and Blue-winged Teal.

Figure 5. Pattern of Age Ratios
in British Columbia for
all Duck Species.

Geographic regions for age ratio analysis

A problem in this study was the division of Canada into regions suitable for age ratio analysis. The primary aim in such a division would be to select areas that are small enough to be homogeneous in the characteristics of interest, large enough that wing samples would be workable, and non-overlapping so that the banding data and wing survey data would be representative of the ~~same~~ groups of birds.

If sets of birds were defined by breeding area then a division into areas for analysis would have been easier. Unfortunately the wing sample refers to a group of birds at the location where they were killed not where they bred. The places where the shot birds bred, or rested during migration (and so were available to be trapped for banding) are unknown. Nor do banding data for most species allow a reliable determination of the source of birds killed in a particular area, because so much of the breeding range is not sampled (Newell and Cooch, 1980).

The method used to define regions was to plot kill locations (weighted for hunting intensity estimated from national kill surveys) from data pooled over an 11-year period for each species reported in the wing samples. A computer drew the maps at a resolution of 10 minutes of latitude and longitude. The maps were visually inspected to select large areas in which each species was killed in a contiguous zone. If wing samples were scattered the region was not considered.

The regions used for age ratio analysis are shown in table 4.

Table 4. Geographic regions used in this study

<u>Species</u>	<u>Region</u>
Common Merganser	Newfoundland Ontario, Quebec and Maritimes
Red-breasted Merganser	from Ontario east
Hooded Merganser	Ontario and Quebec
Mallard	British Columbia Prairie provinces Ontario and Quebec
Black Duck	Newfoundland Maritime provinces Ontario and Québec
Gadwall	Prairie provinces
American Wigeon	Ontario and Quebec Prairie provinces British Columbia
Green-winged Teal	Ontario and Quebec Newfoundland Maritime provinces Prairie provinces British Columbia
Blue-winged Teal	Maritime provinces Ontario and Quebec Prairie provinces

Table 4 (contd.) Geographic regions used in this study

<u>Species</u>	<u>Region</u>
Northern Shoveler	Prairie provinces
Northern Pintail	Prairie provinces Ontario and Quebec British Columbia
Wood Duck	Ontario and Quebec
Redhead	Canada
Canvasback	Canada
Greater Scaup	Ontario and Quebec
Lesser Scaup	Canada
Ring-necked Duck	Canada
Common Goldeneye	Ontario and Quebec
Bufflehead	Canada
Oldsquaw	Ontario and east
Common Eider	Quebec and east

Table 4 (contd.) Geographic regions used in this study

<u>Species</u>	<u>Region</u>
Common Scoter	Ontario, Quebec and the Maritimes
White-winged Scoter	Ontario, Quebec and the Maritimes
Surf Scoter	Ontario, Quebec and the Maritimes

The regions for analysis of age ratios were chosen from this list, although not all data sets were adequate for analysis.

Differential patterns of migration

Hochbaum (1955) discussed the migration patterns of ducks. He argued that a learned tradition formed the basis of migration in adults. Young ducks typically do not associate with their parents in the fall migration, but Hochbaum believed that, after a period of random movement (but responsive to prevailing wind patterns and availability of suitable resting and feeding habitat) young birds find themselves in flocks of ducks that are guided to wintering areas by adults with previous migration experience.

This concept of migration in immatures ducks is largely corroborated by Martinson and Hawkins (1968) who examined banding recovery data from young birds that were known from web-tagging to be broodmates. The available data set was unavoidably small, yet Martinson and Hawkins found that broodmates from Mallard, Gadwall and Canvasback (the only species for which data were available) did not remain associated during the first migration. They credit J.B. Gollop with earlier observations of the same phenomenon. Bellrose and Crompton (1970) develop this further.

This model of migration is consistent with observations of site tenacity at breeding and wintering areas, including a tendency of ducks to return to the place where they were raised (e.g. Lensink 1964). Novice birds have experience of their birthplace but a random component is introduced into their choice of wintering area by the combined effects of a wandering dispersal, wind and habitat conditions, and chance encounters of adult conspecifics that will serve as guides to wintering areas. There is room in this model, too, for immature birds who do not associate with adults, and

either find suitable wintering areas on their own, or who are taken far off course in their wanderings.

Salomonsen (1968) reviews the phenomenon of moult migration. The moult migration is a movement of birds after the initiation of breeding to a place that is suitable for the moult of the remiges. In dabbling ducks it is primarily AM birds that are involved, while some AF diving ducks also take part. As most AM abandon the females during the incubation period they are free to choose a refuge for the flightless period where there may be advantages of safety from predation or reduced competition for food.

Salomonsen does not purport to give a complete description of species that moult in congregations in North America, but among the dabbling ducks he lists mallard, pintail, American wigeon, and green-winged teal.

The extent of moult migration varies within species. The best studies of post-breeding behaviour in adult dabbling ducks are based on radio-tracked individuals. Gilmer et al. (1977) followed the activities of radio-marked mallards and wood ducks in Minnesota and found that all AM mallards left the area for the flightless period, while 48% of AM wood ducks moulted in the study area. About half of the AF mallards left the area during the moult, with wood ducks and successful breeders of both species being the most likely to remain.

A mass dispersal movement of immature birds into an area will increase the age ratios there as determined by the methods of this study. The opposite effect will take

place in areas that attract large numbers of moulting adults (such as Delta Marsh in Manitoba). Unfortunately banding data are limited in the information they can bring to this problem because they can not be used to determine with reliability the composition of birds killed in a particular area as between local birds and immigrants from other breeding areas. The reason is that no banding programs are uniformly distributed throughout the breeding range and there are large parts of all populations breeding in Canada that are not represented by bandings at all (Newell and Cooch, 1980). Birds from these unbanded segments of the population may be numerous in a given area where banding has taken place, and yet not be included in band recoveries.

Despite the biased nature of results from banding, recoveries can still indicate that the dispersal phenomenon exists, although they do not serve to quantify it. Table 5 gives recoveries from all ducks banded as young in the U.S. from 1922 to 1974 that were recovered in Canada before the first migration to the wintering area. This table selects wanderers from the south (in the United States) because most of the analysis regions used in the age ratio calculation were necessarily inclusive of large areas to the north of hunting areas.

Table 5. Evidence from band recoveries of first-seasonal northward movement by young ducks from the United States into Canada

Species	Number of direct recoveries in Canada	Comments
h. merganser	4	
mallard	2549	Ontario north to Hudson's Bay, Quebec, Prairies, B.C.
black duck	1148	Ontario, Maritimes, Quebec, north to 68
gadwall	24	
A. wigeon	24	
g.-w. teal	38	
b.-w. teal	566	Ontario, Quebec, Prairies, Maritimes
shoveler	13	
pintail	265	Prairies, B.C., Ontario, Quebec
wood duck	165	Mostly Quebec, also Ontario

Table 5. Evidence from band recoveries of first-seasonal
(cont.) northward movement by young ducks from the United
States into Canada

Species	Number of direct recoveries in Canada	Comments
redhead	368	Ontario, Quebec, Manitoba
canvasback	52	Manitoba, Ontario
greater scaup	4	
lesser scaup	6	
r.-n. duck	75	Manitoba, Ontario, Quebec
c. goldeneye	85	Quebec, Manitoba
c. eider	10	Nova Scotia (all from Maine)
ruddy duck	2	

Table 5 signals a possible source of young birds into a breeding area before the collection of wing samples by hunters. An effect of this would be unusually high age ratio estimates on a regional basis, even after correction by the methods of chapter 4. To correct for this effect would require a greater amount of banding than is now carried out.

Climatic conditions during the study period

Much of the variability in age ratios is probably related to climate (Crissey, 1969, Geis et al. 1969, Anderson, 1975). As a production index the age ratio reflects the quality of breeding habitat which often reduces to the quantity of available water on suitable substrates. In areas such as the prairies the quality of habitat is known to vary substantially from year to year.

An objective assessment of climatic conditions at the start of the breeding season is available for the Prairie Provinces. May pond counts taken from computer listings from the U.S. Fish and Wildlife Service appear in table 6. They are useful in interpretation of age ratios for prairie breeding ducks.

The relation of climate to production of young and migration patterns is too wide an area for investigation to be covered here with completeness. For such possible effects of climate it is difficult to obtain globally applicable weather data. High precipitation may be advantageous for waterfowl, but not when combined with cold temperature and wind during the hatching period. Steady winds from the southeast may be conducive to dispersal movements, but not if the wind is so strong or temperature so cold that the birds do not fly. For weather data to be useful for waterfowl study, derived variables are required, analogous to "degree days" or "drying indices" used in agriculture.

Without such precise information, the effect of major weather variations can still be identified. Table 7 summarizes the major fall weather patterns for most of the study period. The weather in 1972 is of particular

interest. Thomas (1975) records that that year was the coldest yet noted for Resolute, Chesterfield, and Frobisher Bay (in the Northwest Territories), Goose Airport (in Labrador), and Montreal, among the weather stations he selected for analysis. It was also very cold at Thunder Bay, the only station he selected in Ontario. This cold weather is associated with very low age ratios in many eastern data sets analysed for that year (see chapter 6).

Table 6. Estimates of the number of water bodies in
southern Canadian strata of the May Cooperative
Surveys of prairie breeding areas
(in thousands)

Year	S. Alberta	S. Saskatchewan	S. Manitoba
1971	609	2446	810
1972	651	1958	826
1973	614	1017	260
1974	1496	3120	985
1975	893	2975	719
1976	830	2200	803
1977	423	1155	444
1978	497	2077	923
1979	591	2952	776
1980	610	1057	253
1981	625	597	214
1982	729	1368	282
Mean	714	1910	608

Table 7. Summaries of weather conditions during the study period (from weatherwise 1971-1982)

Year	September			October		
	Prairies	Ont&Que.	Maritimes	Prairies	Ont&Que.	Maritimes
1971	warm dry	warm dry-S. rain-N.	dry sunny end cool	storms end cool	warm wet-N.	sunny dry
1972	cool stormy	normal dry-N.	fair storm in N.B.	cold ₁	cold cloudy	cool wet cloudy
1973	warm rain var.	start hot rain-N.	sunny dry	dry calm	normal frost late in south	dry sunny end stormy
1974	var.	cool wet	rain cloud	fair calm	v. cool sunny	cold snow at end
1975	sunny-W. cool, wet -E.	cool wet	normal end rain	start warm end cool	normal var. rain	cool sunny
1977	wet-S. dry-N.	wet	cool wet	warm dry	warm-N cool-S dry	wet
1978	wet warm	rain-Ont cool-Que	sunny v. cool	dry, sunny-S mild	cool variable	cool wet cloudy
1979	warm dry-S wet-N	cool wet	cool clear	cool-E dry	cool wet	cloudy wet
1981	warm dry	cool wet	cloudy wet			

Realisation of age ratios

To close this chapter on the biological framework of this study it would be good to use data from intensive investigations to show how age ratios in the fall can be derived from clutches of certain size, with certain success rates, and with certain pre-fledging mortality. Unfortunately the elusive nature of waterfowl makes this kind of work very difficult and so only a few results are available.

Ball et al. (1975) report on a study of Mallards and Wood Ducks in Minnesota. They determined that the production per nest was about 4 for Wood Ducks and 4.5 for mallards, after accounting for lost broods. These figures do not account for non-breeding adults. The corresponding age ratios would be 2 for Wood Ducks, and 2.25 for Mallards.

Boyd (1962) gave a diagram reviewing some results on production in selected species. Age ratios may be inferred from the diagram:

Black Duck Maryland 1.2
Black Duck e. Canada 1.8
Blue-winged Teal c. Canada 3.1
Blue-winged Teal Iowa 1.6
Canvasback 2.2
Redhead 2.3
Ring-necked Duck 2.1

These data do not account for non-breeding adults.

These represent localised observations that can not be compared in a detailed way with the wing survey results. Still, they serve to give support to the adjustment methods of the next chapter, which reduce much larger apparent age ratios to figures comparable with these.

THE ESTIMATION OF AGE RATIOS

Chapter 2 opened with a list of factors that may affect the number of wings of each category that are observed in the wing survey. In this chapter 14 models are described that adjust for those factors that can be controlled.

The coefficient of relative vulnerability

The correction of wing survey data for a bias due to relative vulnerability has become a standard practice. The usual procedure is to divide the age ratio (immatures over adults) from the wing sample by the relative vulnerability coefficient determined from banding data:

$$V = \frac{\text{direct recovery rate from immature bandings}}{\text{direct recovery rate from adult bandings}} \quad (11)$$

A detailed discussion of the derivation of V , and similar correction factors is given later in this chapter. The use of a constant V as a correction factor implies 1) that V represents the same ducks as the sample of wings, 2) that an estimate of V pooled over a long period in the hunting season gives an accurate correction even though $V(t)$ if viewed as a function of time may vary significantly during the hunting season, and 3) that the difference in behavior between sex classes is not sufficient to affect the interpretation of V . Some of these questions can be addressed by a comparison of different model results for particular data sets. Others, discussed here, are best considered in the context of estimating V in its own right.

The calculation of age ratios in the models used in this study does not require the explicit use of V . The sampling error associated with V in the models is included through the generation of multinomially distributed band recoveries, but neither V nor its variance is estimated for those models that do use a V implicitly. The discussion of V given here provides a link between previous methods used for age ratio correction, and the methods of this study.

V is the ratio of two proportions, the proportion of immature banded birds that are recovered in the first year divided by the like proportion for adults. The variance of the proportions can be estimated directly (Cochran 1977, p.52). If the proportion is p , from a sample of size n , then the variance of p is, approximately,

$$\hat{\text{var}}(p) = p(1 - p) / n. \quad (12)$$

The variance of the recovery rate from adults or immatures can be calculated with this formula.

$$\text{var}(\text{recovery rate}) = \frac{(\text{recovery rate})(1 - \text{recovery rate})}{(\text{total bandings}) - 1} \quad (13)$$

The variance of the relative vulnerability coefficient itself is not as easy to calculate. Various methods could be used to approximate this, including the jackknife method and the Monte Carlo method as is used for the age ratios in this paper. Seber (1982, p. 388, formula for the variance of r_2) gives an approximate formula for the variance of such a ratio, determined by the delta method. The formula in our notation is:

$$\widehat{\text{var}}(V) = v^2 \left| \frac{1}{AB} + \frac{1}{AR} + \frac{1}{IB} + \frac{1}{IR} \right| \quad (14)$$

where AB are the adult bandings, AR the adult recoveries, etc.

Recovery rates change dynamically during the migration of a particular group of ducks. As an example, the average recovery rates and apparent relative vulnerability of mallards banded in Alberta from 1970 to 1978 vary according to the region of recovery, as shown in Table 8. The results in this table are not applicable to the estimation of age ratios in this study. The relative vulnerability in Table 8 shows the relative likelihood of the two age classes of mallards banded in August in Alberta being killed by hunters in the regions shown.

Table 8. Recovery rates and relative vulnerability (V) of mallards banded in Alberta, 1970 to 1978

Recovery region *	Recovery rates (%)				V
	Adult	s.e.	Young	s.e.	
Alberta	0.63	0.06	3.05	0.14	4.845
Washington	0.40	0.05	0.42	0.05	1.051
Idaho	0.47	0.05	0.39	0.05	0.827
California	0.10	0.02	0.34	0.05	3.244
Oregon	0.18	0.03	0.33	0.05	1.782
Arkansas	0.41	0.05	0.33	0.05	0.800
Louisiana	0.35	0.04	0.31	0.04	0.888
Nebraska	0.36	0.04	0.27	0.04	0.741
Saskatchewan	0.17	0.03	0.20	0.04	1.172
Texas	0.20	0.03	0.17	0.03	0.854
Montana	0.18	0.03	0.16	0.03	0.917
Kansas	0.21	0.03	0.15	0.03	0.717
Missouri	0.12	0.02	0.14	0.03	1.191
Iowa	0.06	0.02	0.12	0.03	2.041
Colorado	0.24	0.04	0.12	0.03	0.499
South Dakota	0.06	0.02	0.11	0.03	1.767
Illinois	0.06	0.02	0.09	0.02	1.474
Mississippi	0.09	0.02	0.09	0.02	0.954
Oklahoma	0.09	0.02	0.07	0.02	0.693
Utah	0.04	0.01	0.06	0.02	1.604
Nevada	0.01	0.01	0.06	0.02	5.614
British Col.	0.02	0.01	0.05	0.02	2.911
Tennessee	0.05	0.02	0.04	0.02	0.832
New Mexico	0.04	0.01	0.04	0.02	1.069
North Dakota	0.02	0.01	0.03	0.01	2.079
Wyoming	0.06	0.02	0.03	0.01	0.567
Minnesota	0.02	0.01	0.01	0.01	0.624
Arizona	0.01	0.01	0.01	0.01	1.248
Total	4.63		7.17		1.549

*arranged in order of young recovery rate.

A 28 X 2 test for independence for the 28 recovery regions as rows and the adult and immature recoveries as columns gave $\chi^2 = 266.38$ (27 df) $p < .001$. This confirms the impression from the table that relative vulnerability of immatures varies substantially among recovery regions. The table is based on a total of 882 adult recoveries and 1095 immature recoveries from bandings of 19063 adults and 15280 immatures.

The table has been arranged in order of decreasing immature recovery rate, and so approximately in order of decreasing recovery sample size. That relative vulnerability should vary among regions is not surprising. It follows from the observations that:

1. to the extent that relative vulnerability is due to the greater naivety of young, the rapid learning after exposure to hunting would reduce the relative vulnerability with time.
2. since the relative vulnerability as calculated here is always based on the original bandings (in Alberta in the table) there will be a tendency for the apparent relative vulnerability to drop with time and distance migrated during the hunting season. This is because the differential relative vulnerability leads to a change in the age ratio, and so a change in the number of each age at risk. In effect the recovery rate of young, relative to the original bandings, must drop as the proportion of young in the population drops.
3. the relative vulnerability of immatures is defined as a ratio of recovery rates. Thus it takes into account factors other than naivety. From table 8 it is apparent

that California is more frequently included in the migration routes of immatures than adults. California ranks 4th among recovery regions for immatures, and 14th among recovery regions for adults. This difference in migration route or timing contributes to a difference in relative vulnerability independently of the ducks' ability to perceive and avoid hunters.

That the relative vulnerability of immatures is higher near the banding location (and so earlier in the season) is a general phenomenon. Table 9 illustrates this, with the only exception being for wood duck in 1971.

Another approach to the analysis of recovery rates is to compare among years using tests of independence. This can be done in two ways, first using $R \times 2$ tables (where R is the number of years included) of the entire series within an age/sex class to test for homogeneity, and second a multiple comparison approach, testing all pairs of years for differences in recovery rate in each age/sex class. In the second approach it is important to increase the precision of the pairwise tests to give a realistic overall error rate (called the experimentwise rate when this conservative approach is taken, following Sokal and Rohlf, 1981). The critical value for g was set at the .001 level of chi-square, $g = 10.828$ (1 d.f.). This reduces the false selection of significant results that would have been likely with many comparisons with a more liberal significance level. It gives an experimentwise error of approximately 10%. Table 10 gives the data used in this analysis, and table 11 shows the results of both approaches. The large values of g in the pairwise tests are not shown. Instead the number of times that each age/sex class in each year was involved in a significant comparison is given.

Table 9. Comparison of relative vulnerability between local region and complete recovery area

Species	Year	Region	Relative Vulnerability	
			within region	all regions
mallard	70	Alberta	2.920	1.764
	71		6.688	1.491
	72		4.828	1.727
mallard	70	Saskatchewan	3.362	1.687
	71		3.922	1.645
mallard	70	Ontario	2.017	1.731
	71		1.723	1.331
	72		1.957	1.586
wood duck	70	Ontario & Quebec	2.322	1.621
	71		1.146	1.487
	72		1.720	1.241

Table 10. Bandings and recoveries of prairie region
Mallards (shot or found dead in the first hunting
season after banding)

Year	AM		AF		IM		IF	
	band.	recv.	band.	recv.	band.	recv.	band.	recv.
1968	4971	51	1758	18	1953	55	1460	26
1969	3195	63	1573	29	5452	203	4861	151
1970	3866	52	1978	32	2915	112	2945	99
1971	4716	48	2136	27	3593	128	3077	97
1972	6715	85	3271	34	4175	188	3255	151
1973	3961	65	1864	17	2117	118	1628	66
1974	3798	39	1566	14	3960	121	3929	103
1975	6469	47	2997	28	4381	147	4017	87
1976	11936	109	5810	59	6695	254	5477	138
1977	14924	128	6141	47	3996	83	3282	62
1978	10294	83	4094	35	5985	138	4685	76
1979	16810	181	4816	46	6239	159	4477	123
1980	13704	116	5583	40	4063	70	3023	51
1981	15461	140	5282	54	2813	55	2060	32
1982	17695	165	5691	58	4772	130	3391	70
total	138515	1372	54560	538	63109	1961	51567	1332

Table 11.

a) Tests of differences in recovery rate of prairie region mallards among years (data from Table 10)

Number of comparisons that were significant ($p < .001$ pairwise)

Year*	AM	AF	IM	IF	V
1969	10	2	6	5	1.78
1981	2	0	7	5	1.91
1980	2	2	8	5	2.11
1968	1	0	1	2	2.31
1977	2	1	7	4	2.40
1978	2	0	6	6	2.45
1979	1	0	5	2	2.51
1970	0	1	5	4	2.51
1982	2	0	2	2	2.57
1974	0	0	3	1	2.87
1971	1	0	5	3	3.08
1976	2	0	6	1	3.40
1973	7	0	12	7	3.49
1975	2	0	4	2	3.52
1972	0	0	7	11	3.83

* - arranged in ascending order of V

b) Tests for overall heterogeneity of recovery rates among years for data of Table 10

χ^2 AM = 56.57 (14 df) $p < .001$

χ^2 AF = 26.95 (14 df) $.025 > p > .01$

χ^2 IM = 167.62 (14 df) $p < .001$

χ^2 IF = 130.455 (14 df) $p < .001$

Thus the recovery rates are shown to be heterogeneous among years in all age/sex classes. The adult female recovery rates are relatively stable. AM recovery rates were certainly distinct in 1969 and 1973. Recovery rates in immatures are highly variable.

The analysis of recovery rates performed here requires a substantial amount of banding to allow detection of differences. Most duck species are not banded in sufficient numbers to give the tests reasonable power. Another data set analysed was for wood duck in Ontario and Quebec. The same 15 years of banding and recovery were included during which the bandings and recoveries were as follows:

	AM	AF	IM	IF
Bandings	3402	938	4968	4133
Recoveries	99	32	239	199

In the wood duck data set only one comparison was found to be significant, that of immature males between 1974 and 1982, with recovery rates of 10/411 and 37/502, respectively. This lack of significance does not prove that wood duck recovery rates do not vary as much as those of mallards in the prairies, however, because of the decreased test power with the smaller wood duck samples. From 1968 to 1982 the relative vulnerability of immature wood ducks varied from 1.081 in 1975 to 3.509 in 1976, a range similar to that of the prairie mallards.

The tests of independence applied to all years of the wood duck data gave:

g AM =	14.88 (13 df)	.1 < p < .5	n.s.
g AF =	9.45 (11 df)	.5 < p < .9	p.s.
g IM =	24.46 (14 df)	.025 < p < .05	
g IF =	21.04 (14 df)	.1 < p < .5	n.s.

Again it appears that recovery rates vary more in immature than adult wood ducks.

It is of interest to test whether recovery rates of immatures differ between the sexes. A test such as this would be expected to give positive results for adults, but there is little evidence for behavior that would lead to differences in susceptibility to hunting according to the sex of young birds. As an example, from the prairie mallard, g-tests on 15 years of band recoveries show 2 significant differences between immature males and immature females in recovery rate. (critical value 8.572 for 1 d.f. and 15 tests using Sidak's multiplicative inequality).

g (IM vs IF 1975) = 11.08
g (IM vs IF 1976) = 15.99

The prairie mallard data set that provided the examples of this section had the relative vulnerabilities shown in Table 12. The relative vulnerabilities in that table are clearly not homogeneous.

Johnson (1974) estimated relative vulnerability by including it as a parameter in a stochastic model of band recovery. He estimated the parameters by maximum likelihood. His method was not appropriate for use in this study, because it assumed a constant relative vulnerability among years, and because V is not used explicitly in the correction models.

Table 12. Relative vulnerability (V) calculated for prairie Mallards

Year*	Relative Vulnerability	Standard Deviation
1969	1.779	0.210
1981	1.909	0.248
1980	2.111	0.257
1968	2.314	0.382
1977	2.398	0.271
1978	2.445	0.282
1970	2.505	0.326
1979	2.507	0.225
1982	2.569	0.252
1974	2.874	0.442
1971	3.082	0.414
1976	3.402	0.316
1973	3.490	0.469
1975	3.517	0.470
1972	3.829	0.412

* arranged in ascending order of V

Accuracy of identification of duck wings

The identification of wings has an associated error that can be significant to the estimation of age ratios. To study this 3 sources of information were used, 1) a control sample, 2) results from birds that had been banded, and 3) additional information provided through the courtesy of S. M. Carney, of the U.S. Fish and Wildlife Service.

The control sample was collected by a select group of waterfowl biologists who had extensive experience with identification of waterfowl, from banding and bag-check projects. The accuracy of identification of the control sample should be much better than identification based on wings alone because the entire body plumage was available, and in addition because the control sample birds were all examined cloacally. The collectors were also experienced in the identification of duck wings as practised at wing bees, so did not lack any available information to distinguish age and sex.

The wings for the control sample were marked in two ways. The envelope used to send the control wings to wing reception centres was given a hunting permit number that was from a range of numbers that did not appear on valid hunting permits. In 1979, 1980, 1981, and 1982 the envelopes and wings were also marked with ultra-violet sensitive fluorescent ink. This allowed verification that the control wing had not become separated from its envelope during the wing bee processing, and also allowed examination after the wing bee of wings that had been identified incorrectly.

It is impossible to control for all types of error. The coding and identification of the control sample is particularly critical. In 1979, the examination after the western wing bee of wings whose classification differed from the control showed an alarming number of errors on mallard wings with distinctive markings that were inconsistent with the control identification. The hypothesis was proposed that a coding error had been made in the control sample. This was an unpleasant turn of events early in this investigation, because it was not clear whether the error should be assigned to the control sample or the wing bee. Since then, additional control samples have shown the error rate to be much less than that indicated by the 1979 western mallard control sample. Further, the questionable sample turned out to be inconsistent with the results of the western wing bee that year. If the errors indicated by the 1979 western mallard control sample had occurred then the observed wing bee results could not have been produced. This was demonstrated when the correction for errors was made (in model C4AF, for example, in notation to be introduced later in this chapter) and produced an impossible negative age ratio. The 1979 mallard control sample had been miscoded, and was not used in analysis of wing bee results. This check on control sample consistency through the matrix inversion models seems to be quite sensitive, as the 1979 control sample results, while appearing erroneous on individual wings, did not seem to be grossly different from other such samples in the large.

Coding and processing errors can be made in the wing bee sample itself. In the case of the control sample comparison this is less of a concern because the control sample wing envelopes were removed from the general survey before processing and were tabulated at least

twice by hand. The kind of troublesome mental error, of thinking "male" and writing "F" is usually caught on the check by a second person. Key entry error rates are kept low by verification, that is the operator enters the age and sex fields twice and the entries must match. A greater threat is in the systematic error introduced by minor, undetected mistakes in computer programs that process the survey data. One such error was found in this study. In 1982 the control sample results were left in with the mass of survey envelopes to have the information extracted later by the computer. (Previous control samples were processed by hand until that year.) During the edit process these records were all flagged as having invalid permit numbers. Under the assumption that it would make no difference (and it should not have done) the records were modified so that they would not appear on the edit listing. Later when the records were extracted for comparison of the control sample results, all the age and sex information had been changed to "unknown unknown". The reason was an obscure error in the survey edit program that caused the loss of the age and sex coding on certain records that were modified by the edit program. This had been happening to a small percentage of the survey records since the development of the edit program about 10 years before. An unhappy series of coincidences meant that the necessary backup tape files had been released, and the control sample information had been lost. Further, a small random sample of useful age and sex data had been lost over the past ten years. There is no reason to think that the losses would in any way bias the age or sex classifications.

2

For the purposes of correction, the aim of the control sample is to give estimates of the error rate in classification. The control sample results are presented in matrix form that shows the number of wings of known category that were identified at the wing bee into each group. The control sample results differ for each species:

AM	AF	IM	IF
called AM	called AM	called AM	called AM

AM	AF	IM	IF
called AF	called AF	called AF	called AF

AM	AF	IM	IF
called IM	called IM	called IM	called IM

AM	AF	IM	IF
called IF	called IF	called IF	called IF

Misclassification Matrix

(Note: the matrix shown here has the columns and rows oriented to conform to the probability matrix on the next page. Later in this thesis the data for this matrix will be displayed with rows and columns transposed.)

This array is reduced to probability estimates by dividing each element by the corresponding column total to give the matrix P:

pr(AM	pr(AF	pr(IM	pr(IF	
called AM)	called AM)	called AM)	called AM)	
pr(AM	pr(AF	pr(IM	pr(IF	
called AF)	called AF)	called AF)	called AF)	
pr(AM	pr(AF	pr(IM	pr(IF	
called IM)	called IM)	called IM)	called IM)	
pr(AM	pr(AF	pr(IM	pr(IF	
called IF)	called IF)	called IF)	called IF)	

The same kind of matrix can be made from the subset of wings that are from banded birds. The envelope used by the hunter to mail his wing has, in the questionnaire area, a place for the hunter to enter the number of a band, if the bird was banded. Also the hunter is asked to return the band with the wing. After the survey is complete it is possible to extract the details of the banding and so identify the species, age, and sex of the duck. In this way a control sample from bandings can be constructed.

This method of estimating the probabilities of identification is much more limited than the control sample from known wings. The reason is that there is no control over the way the hunter handles the band up until the time he mails his envelope. On a day when he

bags only one bird (a fairly common occurrence, 43% of hunters' bags in Ontario in 1979 had only one bird) there are probably few errors. But if he kills several birds, and especially several of one species, the chance of a mix up increases. If he shoots two birds of the same species age and sex he might send the band with the wrong wing, but right category, and so give the correct results. Or someone may transcribe the band number incorrectly.

Accurate information is lacking that would permit the determination of the rate at which hunters send bands that are not matched correctly to wings. A lower bound on this rate is given by the proportion of bandings that are from species that do not match the species of the wing. (Under the criterion that error rate for species identification from the wings is negligible except for special cases that do not obscure this interpretation). Of the 213 cases where band numbers could be matched between the banding recovery files and the wing survey in 1983, 4 showed a species error of which 3 were mallard / black duck mixes. Another estimate of the rate of mismatch that is closer to the true value can be made in species for which we know, based on the wing key or on large control samples, that particular types of error do not occur. In mallards, for example, there was no evidence that adult females are misclassified as adult males. This is probably because the adult female mallard always has well marked white tips on the greater tertial coverts. In a case such as this, results in the control sample based on banding that fall into the "impossible" cell of the identification matrix can be assigned to mismatch error.

In practice the matching of bird bands for a control sample was avoided, except when the matrix could be corrected by removal of mismatches as identified above. It is important to note, however, that the mismatch rates will vary among species, depending on the likelihood that a hunter will have more than one of a species in his daily bag. If a species is rare in the bag the chances are that a mismatch, if it does occur, will result in a species error for which we can reject the comparison. This factor enhances the value of the matched bands for less common species. The less common species are those for which better control samples are deficient, as well.

S. M. Carney (pers. comm.) has experimented with the identification of known age and sex wings in the context of the U.S. wing bees. The results though useful for comparative purposes, may not be directly applicable to the Canadian surveys. One reason is that the persons identifying the U.S. known age material were more experienced at wing identification than most Canadian biologists who have taken part in smaller wing bees over a shorter time period, and who, for the most part, have spent fewer years at this type of work. In addition the United States wings are different from Canadian, in the stages of moult most commonly found, and the relative abundance of the various less numerous species. The U.S. analysis method corresponds to model A in this paper, for which the error rates by category are not as important as the overall effect on the wing sample, and for which compensating errors do not have to be identified. For this reason the U.S. comparison shows only the marginal totals from the identification matrix.

This further restricted the utility of the results for the more demanding models.

The mallard and black duck banding samples illustrate the low frequency scatter of errors that probably reflect envelopes that are not properly matched to the band number. The overall effect is similar to the control sample, however, and the banding identification matrices can be adjusted conservatively by reducing all elements by a fixed amount. In the case of the mallard banding matrix, all elements could be reduced by the maximum of the element and 2, to remove most effects in the banding sample that were not evident in any other control samples. The resulting matrix is:

Species: mallard

Year: 1978 to 82

Type of sample: banding reduced to compensate for mismatches

Known				
AM	48		6	1
Known				
AF		15	1	3
Known				
IM	3		59	3
Known				
IF	1		4	24
	AM	AF	IM	IF

Resulting Identifications

This reduced mallard correction matrix from banding results was used in some of the model calculations for the mallard, with results that were consistent.

The black duck banding matrix is somewhat more puzzling in its form. In part this may derive from the similar appearance of all categories of black ducks, making it harder for the hunter to remember which bird was which in a mixed bag. At any rate the banding results confirm the impression from the control sample that there are serious difficulties in black duck wing identification.

Banding comparisons from some species have been combined into the control sample tables when there was no major disagreement in results.

Control samples that are as yet too small to work with were obtained for common scoter, common and Barrow's goldeneye, common and red-breasted merganser, and northern shoveler.

The common eider table is of little use for correction, but shows the difficulty that arises when birds that can be identified into several age classes are assigned into adult and immature categories.

Appendix 3 gives the misclassification matrices used in this study.

Pooling of control sample data

In many cases the control samples are small enough that there was no option but to combine different years and regions. In these cases there are often not enough data to permit tests for difference between samples. Some of the control samples can be subjected to the G-test of independence (Sokal and Rohlf, 1981). These tests can be applied to the identification of a particular known category into 2 groups (by age, for example) for several control samples. There are normally too many zero cells to use a test of independence among different control samples of the identification into more than two groups. Because of the small sample sizes the Williams' correction (op. cit.) is used.

The following tests were among those performed:

Comparing identification into age classes of:	G	df
(a) AM mallard among all control samples	1.805	4
(b) AF mallard among all control samples based on knowns	12.82 **	3
(c) AF mallard among all control samples except 1979 west, but including banding	3.32	3
(d) IF mallard between known control and banding	2.38	1
(e) IF mallard between known control and banding, excluding 1979 west	5.67 *	1

Comparing identification into
age classes of:

	G	df
(f) IM mallard between known control and banding	2.41	1
(g) IM mallard between known control and banding, excluding 1979 west	1.82	1
(h) AM black ducks between known control and banding	0.122	1
(i) AF black ducks between known control and banding	0.068	1

G is compared with critical values for the chi-squared distribution, which are:

	.1	.05 (*)	.01 (**)
1 df	2.706	3.841	6.635
3 df	6.251	7.815	11.345
4 df	7.779	9.488	13.277

The tests with high values for G were for adult female mallards (b) when the 1979 western data were included, and for immature female mallards. These tests are consistent with the observations made previously that

the 1979 mallard sample in the western wing bee had been miscoded, and that the mallard banding data were inconsistent with the control samples.

There may have been other differences in the types of errors made at wing bees in different years, but the control samples are too small to study such differences systematically. While many of the wing bee personnel have changed, the checkers, who determine the final identification of all wings, have been almost a constant group since 1978. The wing bees may have year to year consistency stemming from the continued use of checkers.

The U.S. control sample

The U.S. Fish and Wildlife Service uses the same identification keys as are used in Canada. The results of their control sample are therefore of interest, even though they may not exactly represent the Canadian wing bees. S. M. Carney (pers. comm.) provided results from a comparison of cloacal (or internal) identifications with wing examinations, shown in Table 13.

The wing bee method tries to classify birds as immature if they are less than 1 year old. A cloacal identification tends to designate as immature all birds that have not yet achieved the age of breeding. For the dabbling ducks the results of both approaches are generally the same. For ducks that mature later there is an intermediate class that is older than one year but not yet breeding. This is reflected in the above totals, which do not include the adjustment for the non-breeding class. Thus the error rate for these species is misleading (being largely a difference in classification of non-breeders) but the data this way better match the Canadian survey results.

**Table 13. Comparison of cloacal and wing classifications
for the United States Fish and Wildlife Service
control sample**

	Cloacally				From wing			
	AM	AF	IM	IF	AM	AF	IM	IF
mallard	399	329	253	213	404	328	243	219
black duck	68	44	164	150	74	41	162	149
gadwall	88	88	93	31	89	89	92	30
American wigeon	161	74	141	168	170	75	133	166
green-winged teal	130	60	105	121	137	62	92	125
blue-winged teal	76	70	76	58	78	71	76	55
shoveler	50	41	71	62	53	40	64	67
pintail	157	123	87	117	157	124	86	117
bufflehead	23	15	33	45	23	12	34	47
common merganser	7	8	31	44	9	11	29	41
red-breasted merganser	27	5	14	9	28	5	13	9
white-winged scoter	83	29	80	75	113	50	51	53
lesser scaup	145	125	148	100	145	122	146	105

Table 13. Comparison of cloacal and wing classifications
 (cont.) for the United States Fish and Wildlife Service
control sample

	Cloacally				From wing			
	AM	AF	IM	IF	AM	AF	IM	IF
ring-necked duck								
	42	25	50	52	41	27	43	58
common goldeneye								
	43	22	47	54	56	28	32	50
Barrow's goldeneye								
	9	13	12	5	9	12	13	5
wood duck								
	43	58	180	171	46	64	176	166
redhead								
	35	23	17	16	34	23	20	14
canvasback								
	20	19	24	44	20	16	25	46
greater scaup								
	100	91	91	115	100	92	92	113
oldsquaw								
	25	25		33	26	23		34
black scoter								
	54	17		78	71	29		49
surf scoter								
	31	20		167	57	45		116
common eider								
	29	34		73	38	40		58
hooded merganser								
	32	22		33	32	22		33

The probabilities of particular misclassifications can not be determined directly from the above table, however, because the total number of errors was also provided for each species, it is possible to set limits on the error rates for age identification (ignoring sex). This is possible because the marginal totals for the 2 X 2 age identification matrix are known, leaving only 1 free cell. The number of errors of age identification must be less than the total number of errors, and this facilitates the enumeration of all possible matrices. Ranges on the error probabilities taken from this enumeration are shown in Table 14.

This table of probabilities should not be confused with confidence intervals for the U.S. control sample, it is only a display of the possible values the U.S. data might generate if they had been gathered and displayed to conform to the 2X2 correction models in this paper.

Table 14. Probability of error in U.S. control sample

Species	Probability of	
	Calling A I	Calling I A
mallard	.003-.038	.013-.069
black duck	.017-.071	.016-.035
gadwall	.011-.028	.032-.056
American wigeon	.009-.038	.039-.061
green-winged teal	.011-.111	.049-.133
blue-winged teal	.014-.110	.037-.142
shoveler	.022-.099	.030-.083
pintail	.007-.025	.015-.034
red-breasted merganser	.031	.087
white-winged scoter	.018-.027	.342-.348
lesser scaup	.019-.052	.008-.044
ring-necked duck	.030-.149	.029-.108
common goldeneye	.031-.062	.208-.228
wood duck	.020-.129	.031-.063
redhead	.052	.061
greater scaup	.010-.073	.015-.073

There is another test of consistency between the U.S. and Canadian control sample results, as is illustrated with the wood duck. Using the probability matrix from the Canadian control sample and the U.S. cloacal data, the expected value of the ~~factor~~ of U.S. wing bee results is calculated:

	AM	AF	IM	IF
calculated U.S. wing sample	46	72	181	153
observed U.S. wing sample	46	64	176	166

Both the observed U.S. wing sample and the calculated result show increases in the AM and AF components compared to the cloacal determination and a decrease in the IF component. The U.S. wing sample had 4 wings fewer than the cloacal determination, while the calculated wing sample showed one more. In general the U.S. and Canadian control samples give consistent results.

Models used for age ratio calculation

The calculation of age ratios involves a set of assumptions that define a model for the correction of various biases in estimation. The age ratio of interest is the number of immatures to the number of adults, just before the start of the hunting season. An estimate of this quantity from wing samples could be generated using a limited set of data for the time period at the opening of the hunting season with correction for relative vulnerability of young, or for errors in identification of wings. It might use only females in the calculations to better represent the reproductive units. To allow a methodological approach to the description of results, 14 basic models were constructed. These 14 models are not exhaustive. They do not, for example, include a selection based on date of kill. The model identifier must be qualified in some discussions, to refer to Model R, September, kill, or Model R, years 1971-1974 pooled, as appropriate.

Abbreviations used for models

Models with no correction of identification errors

Model R - Simple ratio of immatures over adults.

Model F - As Model R, using females only.

Models correcting for relative vulnerabilityRelative vulnerability based on age

Model A - Simple ratio.

Model AF - Females only.

Relative vulnerability based on age and sex

Model AS - Simple ratio.

Model ASF - Females only.

Models correcting identification of age only

Model C2 - Simple ratio of immatures over adults.

Model correcting for relative vulnerability by age

Model C2A.

Models correcting identification of age and sex

Model C4 - Simple ratio of immatures over adults.

Model C4F - As Model C4, using females only.

Models correcting for relative vulnerabilityRelative vulnerability based on age

Model C4A - Simple ratio.

Model C4AF - Females only.

Relative vulnerability based on age and sex

Model C4AS - Simple ratio.

Model C4ASF - Females only.

(Note: female-only models represent a different population parameter than do the others.)

The models numbered in this way provide several hierarchies:

R - F
 R - A - AF
 R - AS - ASF
 R - C2 - C2A
 R - C4 - C4F
 R - C4 - C4A - C4AF
 R - C4 - C4AS - C4ASF

Many comparisons are possible to examine the effects of various model components:

To show the effect of:

Compare:

Age error correction

R to C2
 A to C2A

Use of females only
 (thus estimating
 age ratios only
 for the female sex)

R to F
 A to AF
 AS to ASF
 C4 to C4F
 C4A to C4AF
 C4AS to C4ASF

Age based relative vulnerability

R to A
 C2 to C2A
 C4 to C4A

Age based relative vulnerability

- relative to -

Full relative vulnerability
 based on age and sex

A to AS
 AF to ASF
 C4A to C4AS
 C4AF to C4ASF

To show the effect of:

Compare:

Full relative vulnerability
based on age and sex

R to AS
F to ASF
C4 to C4AS
C4F to C4ASF

Correction of identification
errors of age and sex

R to C4
F to C4F
A to C4A
AF to C4AF
AS to C4AS
ASF to C4ASF

Other comparisons to show particular effects can be similarly determined.

Among the models described the most realistic seem to be models C4AS and C4ASF because they remove all the sources of bias that these models treat. Unfortunately they are also the models that have greatest data needs. Uncertainty is introduced by each attempted correction for bias because the means of correction is from often imperfect information. Proceeding along the hierarchies of models accuracy increases but precision lessens. A primary function of the computer program that calculates estimates is to provide information on the lack of precision due to limited samples in each component of the calculation.

Methods of calculation in the 14 models

I. Age ratio. (used in all models)

Let I = the number of immature wings in the sample
 A = the number of adult wings in the sample then
 the age ratio is:

$$R = I / A.$$

II. Females only. (used in all models that include the letter F in their identifier.) If after corrections have been made the sample still contains information on the sex of wings included, let I_f = the number of female immature wings A_f = the number of female adult wings then the age ratio is:

$$R_f = I_f / A_f.$$

III. Correction for relative vulnerability. The definition of relative vulnerability as a ratio of recovery rates is easily accepted but a more detailed probabilistic derivation is given here to clarify the dependence of relative vulnerability estimates on such complicating factors as variable band reporting rates and trapping biases. More importantly, the derivation allows a generalisation into more than two groups, which is not possible with the usual definition of relative vulnerability.

Suppose that the population of ducks is divided into n subsets $A_1, A_2, \dots, A_n$. Suppose that hunters have killed the corresponding samples $H_1, H_2, \dots, H_n$ within the subsets A_i . Suppose that banders have trapped and banded samples $B_1, B_2, \dots, B_n$ within the subsets A_i . These may be disjoint from the H_i .

Suppose that hunters have killed the corresponding samples $K_1, K_2, \dots, K_n$, within the subsets B_i . K_i is thus a subset of H_i . Suppose that the probability that a hunter who has killed a banded bird actually reports it is P , and that the samples of recovered bands are $S_1, S_2, \dots, S_n$, where $S_i = K_i \cap P$, etc.

We wish to estimate the relative vulnerability of subgroup r compared to subgroup s :

$$V_{rs} = \frac{\text{prob(a bird in subset } r \text{ is killed)}}{\text{prob(a bird in sub set } s \text{ is killed)}}$$

Each probability can be estimated as a fraction:

$$V_{rs} = \frac{H_r / A_r}{H_s / A_s} \quad (15)$$

The ratio H_r / A_r can be estimated from what we know happened to B_r , a subset of A_r . Note that in doing this we assume only that the sample B_r is representative of A_r , we need not assume that the different subgroups are equally likely to be banded:

$$H_r / A_r = (S_r / P) / B_r \quad (\text{estimated}). \quad (16)$$

$$\text{Therefore} \quad V_{rs} = \frac{S_r B_s}{S_s B_r} \quad (17)$$

V_{rs} is called the relative vulnerability of subgroup r to subgroup s .

Suppose, now that a sample of wings, $W_1, W_2, \dots, W_n$ is to be used to estimate ratios of the $A_1, A_2, \dots, A_n$. Thus,

$$R = \frac{A_1 + \dots + A_r}{A_{r+1} + \dots + A_s} \quad (18)$$

is to be estimated.

Suppose that Q is the probability that a duck that has been killed will have a wing removed and sent into the survey. If Q is assumed to be constant among the n subsets, then

$$W_r / H_r = W_s / H_s = Q \text{ (a constant)}. \quad (19)$$

So $H_r = W_r / Q$ can be substituted in the equation 16:

$$\frac{W_r}{Q A_r} = \frac{S_r}{B_r P} \quad (20)$$

This provides the correction for relative vulnerability as applied to the above definition of R in equation 18. Solving equation 20,

$$A_r = \frac{W_r B_r P}{Q S_r} \quad (21)$$

and substituting into equation 18,

$$\hat{R} = \frac{\frac{W_1}{S_1} + \dots + \frac{W_r}{S_r}}{\frac{B_1}{S_1} + \dots + \frac{B_r}{S_r}} \quad (22)$$

$$\frac{W_{r+1}}{S_{r+1}} + \dots + \frac{W_s}{S_s}$$

The significance of the term, relative vulnerability, is apparent in the case where there are only two subsets in the above ratio. Thus if immatures comprise one subset and adults the other, a simple expression for the corrected ratio is:

$$R = \frac{A_I}{A_A} \cdot (1 / V_{IA}), \quad (23)$$

or, in the simpler notation we have been using,

$$R = \frac{(I / A)}{V} \quad (23a)$$

When, as in the age and sex based correction for relative vulnerability, there are more than one subsets involved in the numerator or denominator, V_{rs} is not used explicitly in the correction.

Models that include A, without S, in their identifiers perform this correction based on the subsets adult and immature. Models that contain AS in their identifiers perform this correction with the four age/sex subsets, using equation 22.

IV. Correction for errors in identification

Consider a sample of wings that have been identified. The correction for errors in identification starts with a matrix of identification of a control sample of known age and sex.

(M_{rc}) = number of wings known to belong to category c that were identified as being in category r .

This matrix is modified by the division of each element by the corresponding column total to give P , now a matrix of estimated probabilities:

(P_{rc}) = probability of a wing in category c being identified as being in category r .

M and P are $n \times n$ matrices, where n is the number of categories

If the correct identifications are given by the vector $\underline{w} = (w_1, w_2, \dots, w_n)$ then the matrix product $P \underline{w}$ gives the expected values for the number of wings assigned to each category according to this model of misclassification.

$\underline{X} = P \underline{W}$ = vector showing sample in each category, as identified. (24)

Our best estimate of $\underline{W}$, given $\underline{X}$, is found by reversing this procedure:

$$\underline{W} = \underline{P}^{-1} \underline{X} . \quad (25)$$

This is the method used to correct for identification errors. Either a 2 X 2 or a 4 X 4 matrix of probabilities is formed, depending on whether a particular model uses information on sex as well as age class. The matrix is inverted (in the results shown here the inversions were done by the Gauss-Jordan elimination method). The product of the inverted matrix by the sample vector gives the corrected vector.

It is possible that P might be singular, in which case this correction can not be done. If, for example, the wing identifiers classified all wings as immature then P could not be inverted and age composition could not be regained from the sample.

Calculation of variance and other measures of precision

For a few of the 14 models it is possible to estimate the precision of estimates by direct calculation. In model R, for example, the age ratio is calculated as a fraction I / A. We could therefore express the ratio as a proportion and estimate the variance by the usual expression:

$$\text{proportion } P = R / (1 + R) \quad (26)$$

$$\text{Variance of } P \approx P (1 - P) / N. \quad (27)$$

(This formula would not give the same result as model R because it ignores the sex of the birds. It assumes a binomial distribution, while model R represents the sample as multinomially distributed according to 4 age/sex categories).

It is not easy to derive variance formulas for most of the other models, in particular those models that correct for identification errors and involve the inversion of a matrix. This is a non-linear calculation step for which no exact variance formula exists. One way to estimate the precision of a non-linear statistic is to generate a series of samples such as would be expected from many repetitions of the same experiment under the same conditions. This replication approach was used for the age ratio models.

All the models are based on a sample of wings, received in the four categories AM, AF, IM, and IF. For the simulation of results the total sample size, $AM + AF + IM + IF$ is fixed, and a new sample is generated according to a multinomial distribution with parameters AM / total , AF / total , etc.

For models that use relative vulnerability corrections based on banding data (either for two or four categories) the total number of bandings in each category is taken as fixed and the number of recoveries is generated as a binomial variable with parameter p , the proportion of recoveries in the original sample.

Models using correction of identification errors via a control sample matrix are generated according to a multinomial model. The total number of wings in each known group is kept constant which means that the column

totals in the control sample matrix are fixed. The number of wings assigned to each element within the column are multinomially distributed with parameters given by the proportions in each column of the original matrix.

In all cases the observed proportions were used as the estimates of the corresponding population parameters:

1. the proportions of the four categories of identified age and sex.
2. the recovery rates of each age/sex category.
3. the rates of correct and incorrect identification of each category, supposing that the rates are fixed according to result category.

Behavior of the models

Some of the models for ratio estimation have a mathematical form that is non-linear and might have behavior that is difficult to predict. In particular the models that correct for identification error include a matrix inversion that may be unstable in the sense that minor variations in the input data may lead to large differences in the result. There is no reason to expect that the results from these models should be distributed normally, and so inferences based on the standard error of the simulated ratios may be invalid in the event that the distribution is heavily skewed.

The computer program that carries out the estimation responds to hypersensitive models by dropping them from consideration in the analysis of particular data sets. If a particular set of simulated values for wing receipts, banding recoveries, and control sample leads to an invalid result, the trial is marked as invalid for

the model in question. After every 100 trials the proportion of invalid results is checked, and if it exceeds 20% the model is abandoned for use with the current data set. This provides a sensitivity check on the model relative to the available data.

The reasons for classifying a trial as invalid for a particular model follow (these are termed the validity criteria).

1. Impossible calculation steps. This includes division by zero in relative vulnerability correction, singularity of the matrix used for identification error correction, and division by zero in the result.
2. Computational artifacts. This refers to the production of negative results by models that use matrix inversion. These results show inconsistency between the control sample and wing sample, but are not meaningful as age ratios.
3. Biologically unrealistic results. The program rejects age ratios less than 0.01 or greater than 12.

The computer program displays 3 measures of central tendency for the simulated results. These are the mean, the median, and the value that results from substitution of the parameters used for generation of the pseudo-random variables. This third measure of central tendency is of special interest as the estimate of corrected ratios that is obtained by direct calculation

without simulation. For some models it corresponds to the mode, but this is not generally true. For purposes of discussion it is termed the central value.

In view of the skewed nature of most of the distributions resulting from the simulations a trimmed mean might also have been used (Bickel and Doksum 1977). The corresponding measure of spread would be the Winsorized sample variance (loc. cit.). The differences among the measures of central tendency from the simulations were not large enough to necessitate the use of this more robust but often misunderstood estimator.

The program also calculates 3 measures of spread. These are the range, the variance, and the interval from the 5%-tile to the 95%-tile. In most runs the range was artificially limited to (0.01, 12.0) by the validity criteria, but in practice these extremes were rarely achieved (models achieving these limits usually did so often enough to be rejected). The variance was expressed in 3 ways, as itself, as its square root (the standard deviation) and as the coefficient of variation (the standard deviation divided by the mean). The measure used most often is the 5%-tile to 95%-tile interval, which was taken to estimate a 90% confidence interval for the calculated ratio.

In some runs different versions of the program were used to investigate aberrant behavior of the models with sparse or unusual data sets. In some cases the range of results was not restricted. In other cases a grouped frequency distribution of results was displayed.

Wood ducks in Ontario and Quebec in 1976 illustrate the behavior of the models with poor data sets. (Tables 15, 16). These data were analysed by a version of the

estimation program that did not reject results according to the biological criteria. In that year the sample comprised:

Wing sample	AM 22	Banding recoveries	AM	5 / 187
	AF 12		AF	4 / 55
	IM 36		IM	12 / 313
	IF 27		IF	11 / 259

The usual identification control sample for wood ducks was used.

Table 15. Measures of central tendency for wood duck in
1976 Ontario and Québec

Model	Central value	Mean	Median
R	1.85	1.90	1.85
F	2.25	2.52	2.31
A	1.71	1.83	1.68
AF	2.08	2.44	2.11
AS	1.59	1.68	1.51
ASF	3.85	4.95	3.97
C2	1.99	2.11	2.00
C2A	1.84	2.03	1.79
C4	1.98	2.10	2.00
C4F	3.21	5.85	3.37
C4A	1.83	2.03	1.79
C4AF	2.97	5.62	3.02
C4AS	1.61	1.76	1.55
C4ASF	5.50	11.22	5.76

Table 16. Measures of spread for wood duck in 1976Ontario and Quebec

(all standardized to the mean)

Model	5% to 95%-tile	C.V.	Range
R	0.75	0.22	1.47
F	1.15	0.46	7.03
A	1.48	0.48	4.02
AF	1.81	0.65	9.70
AS	1.63	0.54	4.85
ASF	2.12	0.92	17.54
C2	1.03	0.32	2.72
C2A	1.60	0.55	5.21
C4	1.03	0.32	2.60
C4F	2.43	2.40	43.80
C4A	1.60	0.54	5.01
C4AF	2.58	2.23	39.91
C4AS	1.73	0.58	5.39
C4ASF	2.89	2.22	33.64

The simulation for the wood duck data set generated unrealistic outliers, especially for models that were based on age ratios restricted to females. The usual version of the estimation program would have rejected such values, and rejected the models themselves if the rate of invalid results exceeded 20%. It is unlikely that the mean and variance of simulated results for such a data set would have stabilized after 1000 trials, so there may be a significant error introduced by the limit on trials in the program, for such a data set.

The mean exceeds the median and the central value in all cases, as is characteristic of distributions skewed right. A longer right than left tail occurs in almost all the age ratio calculations performed. Most simulations do not include the artificial cutoffs at .01 and 12 in their ranges, so this is not an important contributing factor to the skewed distribution of values. More important are various facts stemming from mathematical, biological and sampling limitations that lead to the generation of results with greater deviation to right than to left of the median. One such fact is that the range of possible age ratios from 0 to 1 corresponds by a change of labels from A to I and vice versa to a range from 1 to infinity. The skewness of results from models 1 and 2 stem from this effect, which is analogous to the skewed nature of the binomial distribution. The models using relative vulnerability correction from banding data might show the opposite effect, as they involve division by a coefficient, V , which is mathematically constrained to the interval $(0, \text{infinity})$ but which, for biological reasons is usually greater than 1. However the behaviour of $1/V$ in simulated data sets reflects the relative sample sizes contributing to its numerator and denominator. The numerator is the adult recovery rate which is typically

based on much smaller samples than that of immatures and so the skewed right nature of the binomially distributed adult recoveries predominates in the generation of unusual results. The generation of results through the control sample matrix is more difficult to predict. There is a tendency for adults to be misclassified as immatures so a very simple discussion of model behaviour can be taken from the matrix:

A called A 0 ---

A called I I called I

If this matrix is used to correct an age ratio, I/A, the modified age ratio has the form:

$$R = \frac{I \text{ pr (A called A)} - A \text{ pr (A called I)}}{A} \quad (28)$$

(The appearance of this formula is slightly confusing in that it consists of a modified value of I divided by the original value of A. In the derivation a common factor has been cancelled. In fact the correct number of adult wings is $A / \text{pr(A called A)}$).

Now the probabilities above are estimated from a control sample. If the total number of adult wings in the control sample is S, and if of these C were identified correctly and E were identified incorrectly then:

$$R = \frac{C \cdot I - E \cdot A}{S \cdot A} \quad (29)$$

We can now examine the effect of generation of different values in the control sample. If the simulated value of C is one greater than the central value then E must be one less, because $C + E = S$ is constant in the simulation. Let R_1 be the value of the age ratio resulting from an increase by k in C , and R_2 the age ratio resulting from a decrease by k in C . Then

$$R_1 - R = R - R_2 = \frac{k(I + A)}{S \quad A} \quad (30)$$

This means that in this case there is no additional tendency for skewness from the functional form of the age ratio correction with the control sample. The multinomial distribution used in the simulation will however produce a skewed distribution of deviations from the central value which will again produce a longer tail to the right than left in the distribution of simulated values.

The general effect of error correction on the distribution of simulated results is much less tractable than in this example, so an empirical approach is the easiest way to study the distribution of the model results in question. In practice when the model using the matrix correction leads to a strongly skewed distribution the number of invalid trials is sufficiently large that the computer program drops the model from application to the offending data set.

The wood duck example provided above shows how the models behave with extraordinary data. Most data sets do not create extreme outliers in the simulation. An example of a regular data set is that for mallards in the prairie provinces in 1976. In that year the sample comprised:

Wing sample	AM 113	Banding recoveries	AM 109 / 11936
	AF 120		AF 59 / 5810
	IM 452		IM 254 / 6695
	IF 325		IF 138 / 5477

The identification control sample using all results except 1979 and 1980 western wing bee samples was used. Results are shown in Tables 17 and 18.

Table 17. Measures of central tendency mallard 1976
prairie provinces

Model	Central value	Mean	Median
R	3.33	3.35	3.35
F	2.71	2.74	2.74
A	0.98	0.99	0.98
AF	0.80	0.81	0.80
AS	1.03	1.03	1.02
ASF	1.09	1.11	1.10
C2	2.93	2.98	2.92
C2A	0.86	0.88	0.86
C4	2.84	2.89	2.84
C4F	2.02	2.08	2.03
C4A	0.83	0.85	0.84
C4AF	0.59	0.61	0.60
C4AS	0.88	0.89	0.87
C4ASF	0.82	0.84	0.81

Table 18. Measures of spread mallard 1976 in the prairie
provinces
 (all standardized to the mean)

Model	5% to 95%-tile	C.V.	Range
R	0.24	0.07	0.44
F	0.34	0.10	0.66
A	0.39	0.12	0.73
AF	0.46	0.14	0.91
AS	0.40	0.12	0.72
ASF	0.59	0.18	1.25
C2	0.45	0.13	0.86
C2A	0.54	0.17	1.03
C4	0.47	0.14	0.88
C4F	0.63	0.20	1.46
C4A	0.57	0.17	1.10
C4AF	0.70	0.22	1.70
C4AS	0.59	0.18	1.20
C4ASF	0.83	0.25	1.99

If the results were distributed normally then the median would equal the mean. Further, the expected ratio of the 5%-tile to 95%-tile interval over the standard deviation would be $2 \times 1.65 = 3.3$. Rohlf and Sokal (1981) give a table of expected values of the range of a sample from a normal distribution. A sample of 1000 has an expected value of the range of 6.48 standard deviation units. The table of measures of spread would, in the normal case, have values in the approximate proportions 3.30:1:6.48. This approximation is well matched by the mallard example. The wood duck example, although close in the size of the 90% confidence interval to the normal approximation, has a range that is much larger than expected in the models that developed unrealistic outliers. When the model behaved in this way the 90% confidence interval for wood ducks seemed less than would be predicted by the normal approximation. In fact this could be a result of the distortion of the variance by the outliers. An improved estimate of the C.V. might be the Winsorized sample variance mentioned above.

Summary of error corrections used

At the start of Chapter 2 some factors to consider in the interpretation of age ratios are listed. Using the methods of Chapters 3 and 4 some of these can be dealt with to some extent. This summary shows which corrections can be made. The same numbering is used as in Chapter 2.

2. The age composition reflects the makeup of the

population in the region of study before the start of the hunting season. It may therefore include a disproportionate number of some age or sex class when the preseason dispersion and migration are heterogeneous. Many birds shot in the study regions are from banding areas where no birds have been banded. Table 5 shows that substantial numbers of ducks move north from the U.S. into Canada, where they are at risk to hunting. This remains an important source of error.

5. The true composition in the population is not represented accurately in the wing sample because the classes differ in vulnerability to hunting and so are reported at different rates. The models performing relative vulnerability corrections (those with the letters 'A' or 'AS') adjust for this effect. Their effectiveness is limited by the quantity and representativeness of band return data.

6. The identification of wings at wing bees has errors that distort the apparent composition of the sample. The models performing misclassification correction (those with the numbers '2' or '4') correct for this effect. Their effectiveness is limited by the available samples of known age and sex wings that were identified. It is not known whether larger control samples are needed to allow for variation in misclassification among years.

7. The sample differs in composition from the population because of chance. Estimates of the size of this error (such as the standard error) are produced for the various correction methods.

8. The sample does not represent a homogeneous population in time. Age ratios do vary in time (Figures

2-5). The sample is concentrated early in the hunting season, which is advantageous for the models that correct for relative vulnerability, if only because a longer time period makes the correction model less realistic.

9. The hunter may not send a representative sample of his kill. A field survey of hunters could produce a sample of people who were also chosen for the wing survey. Since less than 1% of all Canadian hunters are chosen and respond to this survey, the useful information from a haphazard attempt is limited. Also, if the hunter is in a party of more than one, if he hunts in more than one place the day he is interviewed, or if he reports the wrong date of hunting, the results are ambiguous. No results of such a field validation of this survey are now available.

10. Because the survey is based on a selection of hunters and not wings a low within-hunter variance may allow a false impression of precision. This is an important consideration that is discussed more fully in Appendix 7. Modifications to the survey were made in 1984 so that, after 1985, a cluster-based analysis will be possible.

11. Errors may be made in the processing of survey material, the coding of results, and the computation of estimates. It is hoped that this demonic source of error has minimal effect.

5 Other Topics: Sex Ratios and Change-in-ratio Method

Two areas of other possible use for the wing survey data are examined. This discussion is separate from the results presented in Chapter 6, and may be read independently.

Sex ratios

Much of the published material dealing with the composition of the kill of ducks by hunters relates to the sex ratio, that is the ratio of males to females. One reason for the concentration on sex, rather than age ratios, is from the relative ease of field identification of sex, particularly in adults. Also there is a more obvious complication of relative vulnerability between adults and young than between the sexes, so that a sex ratio from hunter-killed birds might be considered to be more representative of the wild population than an age ratio would be. The sex ratio has been used to characterize survival through an argument that differential mortality of the sexes, operating on a sex ratio of 1 at hatch, causes the adult sex ratio to be a function of adult survival. (Bellrose et al., 1961).

A useful summary of knowledge of duck sex ratios is given by Aldrich (1973), who drew heavily on an unpublished paper by A. Dzubin. Much of the concern over sex ratios at that time centered on a discussion of the possibility of using hunting regulations to purposefully reduce what seemed to be an overabundance of males, in the hope that improved breeding efficiency would result. Aldrich's paper emphasized the uncertainty of our knowledge of the role of "excess" males, and our ability

to manipulate the sex ratio through management.

Sex ratios remain of interest, despite the number of unanswered questions. Studies of breeding behavior can provide better knowledge of the role of excess males (Humburg et. al. 1978 describe a study on mallards). In view of the continued interest in sex ratios the mathematical approach already developed for age ratio analysis was adapted as a tool for the interpretation of sex ratios.

In the development of the models for correction of age ratios, the age categories were given no particular significance except as identifiable subsets of the population. It is appropriate, then, to use the same models to analyse ratios between other subsets of the population, and, in particular, for the analysis of sex ratios.

For sex ratio analysis it is convenient to identify adult with female and immature with male.

Under this change of labels the age ratio models will provide estimates of the sex ratio as males / females. The 14 models have the following new interpretations (numbered to correspond, in order, to the models of Chapter 4):

1. Unadjusted ratio males / females in wing collection.
2. Sex ratio of adults only, unadjusted.
3. Sex ratio corrected for relative vulnerability between males and females.

4. Sex ratio corrected for relative vulnerability between males and females, ratio for adults only.

5. Sex ratio corrected for relative vulnerability among all 4 age / sex categories.

6. Sex ratio corrected for relative vulnerability among all 4 age / sex categories, ratio for adults only.

7. Sex ratio corrected for identification errors involving sex only.

8. Sex ratio corrected for identification errors involving ~~sex~~ only, and corrected for relative vulnerability between the sexes.

9. Sex ratio corrected for all identification errors.

10. Sex ratio corrected for all identification errors, ratio for adults only.

11. Sex ratio corrected for all identification errors, and for relative vulnerability between the sexes.

12. Sex ratio corrected for all identification errors, and for relative vulnerability between the sexes, ratio for adults only.

13. Sex ratio corrected for all identification errors, and for relative vulnerability among all 4 age / sex categories.

14. Sex ratio corrected for all identification

errors, and for relative vulnerability among all 4 age / sex categories, ratio for adults only.

The common pattern among adult ducks is that males outnumber females, so the expected age ratios are greater than 1. The tertiary sex ratio, which is the number of males divided by the number of females at the age of fledging, does not show significant departure from 1, according to numerous field studies of birds banded as locals (not yet flying, or so newly fledged that a dispersal movement has not occurred. See Aldrich, 1973 for some references in which all ratios quoted are near to, but greater than 1. Munro and Kimball, 1979 also obtained a value near 1.) If the pattern holds, then, we should expect that the models giving adult sex ratios should give larger sex ratios than the models that combine age classes. We should see model 4 > model 3, model 6 > model 5, model 2 > model 1, model 12 > model 11, model 10 > model 9, and model 14 > model 13.

It does not always happen that the wing receipts show a greater departure from a balanced sex ratio in adults than young. When it does not, we may be interested in confidence limits on the estimate of sex ratio in young, rather than adults, to test whether the tertiary sex ratio as indicated by hunting kill is in fact significantly different from 1. To do this with the same computer program a further change of labels is needed, because the age ratio program does not address age ratios restricted to the male sex. If immatures are identified with females, models 2,4,6,10,12 and 14 produce confidence intervals for sex ratio in young.

Only one of this last type of analysis was performed, for illustrative purposes. The data set used was for

mallards killed any time of the year in the 1979 hunting season in the prairie provinces. Banding data for relative vulnerability correction models was from 1979 bandings in the same region. The correction for identification was pooled from all valid control samples.

90% confidence limits on sex ratio of
immature mallards in the prairie
provinces, 1979.

Model	5%-tile	Mean	95%-tile
2	1.096	1.219	1.303
4	1.232	1.489	1.824
6	1.043	1.300	1.649
10	0.976	1.223	1.583
12	1.132	1.494	2.041
14	0.973	1.305	1.826

Change in ratio methods

The population model in the introduction demonstrates how the greater exploitation rate for immature ducks leads to a change in the age ratio during the hunting season. The amount of change in the ratio depends both on the number of young birds being killed relative to the number of adults, and on the total population size. Various estimation procedures are available that make use of changes in ratio between two components of a population that are exposed to different removal rates. It is important to note that without banding data from during the hunting season, the estimation of age ratio late in the season is of questionable merit. In addition, the possibility of bias in harvest surveys,

the possible sampling, relationship between the wing survey and the harvest survey results, and the movement of birds during the hunting season all weaken the use of this method for ducks with existing data. The calculations here are only illustrative.

Seber (1982) reviews the change in ratio methods. Suppose there are two sampling occasions, at $t = 1, 2$. Let X denote adults and Y denote young. Let

- X_t = # of immatures at $t = 1, 2$
- Y_t = # of adults at $t = 1, 2$
- N_t = total population at $t = 1, 2$
- $P_t = X_t / N_t$ the proportion of immatures at time $t = 1, 2$
- $R_x = X_1 - X_2$ the number of removals of immatures
- $R_y = Y_1 - Y_2$ the number of removals of adults
- $R = R_x + R_y$ the total removals
- $f = R_x / R$ the proportion of removals that are immature
- u, u_x, u_y exploitation rates in total, and for immatures and adults
- $\gamma, \gamma_x, \gamma_y$ corresponding instantaneous exploitation rates
- x, y, n small letters denote sample values

This notation applies only to the discussion of change in ratio methods, where R is not to be confused with the use of R to denote the age ratio elsewhere in this report. The usual age ratio corresponds to P_1 in this notation by the formula:

$$P = (\text{age ratio}) + (1 + \text{age ratio}).$$

The wing survey provides estimates of P_1 required for these methods. An estimate of removal is needed. For this purpose kill statistics from the Canadian migratory game bird harvest survey are useful. These survey results are estimates, and will contribute to the variance of values calculated by the change in ratio method (see Seber 1982 p. 371), but for purposes of illustration removals are assumed to be known. In fact, while total kill of ducks is measured by a questionnaire survey independent of the wing survey, the kill by species is determined in part from the same wing sample used here. A careful use of the change in ratio method should consider dependence between estimates of P_1 and R.

Formulas given by Seber for the closed population case provide estimates of population size, proportion of young, and variances (formulas 9.2 p. 354 and 9.3, 9.4 p. 355), and exploitation rates and variances (formula 9.26 p. 380).

The prairie provinces mallard in 1971 can be used to illustrate the change in ratio methods. The two sampling periods from the wing survey were September and the rest of the hunting season (Late). The wing age ratio for September was corrected for relative vulnerability in the normal fashion, using band recoveries from September only. An estimate of the late age ratio is not as easy to obtain. Figure 2 shows how wing age ratios change during the season in the prairie provinces. It shows very large wing age ratios in September, and a rather abrupt change to a lower level later. This does not conform to a model of constant relative vulnerability leading to a steady decrease in wing age ratio (compare with figure 4). For this calculation the late wing age

ratio was corrected by using band recovery rates during the late time period. This means that the adjustment was made on the basis of the relative probability of the two age classes to be killed, from birds banded before the hunting season. It could be argued that the lack of banding data from during the hunting season means that the adjustment leads to an estimation of the preseason age ratio, but this argument does not hold in a regional situation such as this where different components of the banded population have different risks of being killed at different times of the season. The mallards that are subjected to the greatest hunting pressure in September have largely left the region by the second time period. (Bellrose and Crompton, 1970, show two main waves of mallard migration in the Canadian prairies for birds banded in Illinois, the main wave in September, and secondary wave or waves in October. They show the Canadian population represented by their banding peaking September 20-26).

The migration of birds from the region both violates the requirements of the change-in-ratio method, and it adds uncertainty to the use of banding data to correct age ratios.

The season kill of mallards in the prairie provinces in 1971 was about 1,500,000. This was allocated to young and adult based on the year's sample of wings. (1,084,000 young, 416,000 adult). The variance of f was estimated as if it were a binomial variable. The remaining values needed were:

	Sept	Late
Adult wings	134	463
Young wings	589	967
P	.488	.450

The estimates of global parameters were:

Population at start of hunting season 10.8 million
(s.d. 6.2 million).

Young at start of hunting season 5.25 million
(s.d. 2.8 million).

Overall exploitation rate 13.9% (in Canada)
(s.d. 6.8%).

Exploitation rate for young 20.6% (in Canada).

Exploitation rate for adults 7.5% (in Canada).

The precision of these estimates is poorer than shown because of the simplifying assumptions that were made. Most such analyses would be less precise than for the prairie mallard. Further, a potentially large and unknown source of bias may be present in the harvest survey results.

6 RESULTS OF AGE RATIO CALCULATION

The depth of analysis possible with the methods of this study varies depending on the quantity of information available, and the quality of results (i.e., the number of valid simulations under the different models).

16 data sets have been analysed, as described in this chapter.

- 1) Prairie Mallards (from Manitoba, Saskatchewan, and Alberta.
- 2) Black Duck from the Maritime Provinces (Nova Scotia, Prince Edward Island, and New Brunswick).
- 3) Black Duck from Ontario and Quebec.
- 4) Wood Duck from Ontario and Quebec.
- 5) Mallard from Ontario and Quebec.
- 6) Blue-winged Teal from Ontario and Quebec.
- 7) Pintail from the Prairie Provinces.
- 8) Blue-winged Teal from the Prairie Provinces.
- 9) Gadwall from the Prairie Provinces.
- 10) American Wigeon from throughout Canada.
- 11) Bufflehead from throughout Canada.
- 12) Hooded Merganser from throughout Canada.
- 13) Redhead from throughout Canada.
- 14) Lesser Scaup from throughout Canada.
- 15) Ring-necked Duck from throughout Canada.
- 16) Canvasback from throughout Canada.

1) Prairie Mallards

From the point of view of analysis the prairie mallard is of particular interest. The main reason for this is that the samples of wings and banded birds are large relative to what is available for other species.

Twenty-eight types of analysis were performed for the prairie mallard. The 14 models were used on the full years' wing samples and banding samples. Also, to study the effect of a short time frame for sampling, the 14 models were used to analyse age ratios from wing and banding data from September only.

The control sample used for this analysis included all known mallard wings from 1978, 1979 (eastern wing bee only), 1980 (eastern wing bee only), and 1981. In addition the banding comparison control sample was used, after modification to remove suspected misidentifications as discussed in the section on control samples from banding. (Chapter 4.)

Banding data used included all mallards banded in the prairie provinces for which age and sex were determined. The recoveries included were from birds shot or found dead in Alberta. For the September only calculations band recoveries were limited to that month as well. The banding data for this series of calculations is discussed in more detail in the section on band recovery rates. (Chapter 3).

Wing sample data from all survey responses that indicated the prairie provinces as the region of kill are shown in Tables 19a (for the full time period) and 19b (for September kill dates only).

Table 19a. Wing sample for analysis of age ratios of mallard in the prairie provinces

Year	AM	AF	IM	IF
1971	332	265	825	731
1972	287	302	596	537
1973	168	117	395	354
1974	121	81	327	230
1975	73	82	250	276
1976	113	120	452	325
1977	149	78	289	270
1978	154	93	355	267
1979	220	196	482	394
1980	150	129	311	265
1981	202	118	308	211
1982	130	100	222	184

Table 19b. Wing sample for analysis of age ratios of mallard in the prairie provinces, September kill dates

Year	AM	AF	IM	IF
1971	70	64	313	276
1972	105	120	295	274
1973	33	27	169	135
1974	10	0	50	31
1975	9	8	73	89
1976	34	30	154	120
1977	4	6	59	32
1978	11	4	60	48
1979	70	53	180	164
1980	52	49	130	109
1981	75	33	133	93
1982	20	17	44	37

The results of age ratio calculation for prairie mallards are shown in figures 6 through 17. These graphs show the performance of all 14 models in the given year. The model identifier is on the vertical axis. The horizontal axis shows the age ratio, from 0 to 8. (Age ratios greater than 8 are so unlikely that the diagram does not need to show them). The centre mark on the horizontal lines is the mean of the age ratios produced by the simulation. The end marks are the 5% and 95% percentiles of the simulation results. They can be interpreted as 90% confidence intervals for the age ratio.

Some overall comments apply to the results from the various models. The models that do not include correction based on banding give results much larger than other models, showing that the effects of relative vulnerability between classes is important. The differences between other results are generally smaller when it is not a question of performing or ignoring the banding based correction. Model A and model AS give similar results, showing that for prairie mallards the correction for relative vulnerability based on age only is adequate. The control sample models have lower age ratio results than the others, showing a small but consistent bias due to errors of identification. The effect of misidentification, however, is smaller than the uncertainty introduced by sampling effects as represented by the confidence intervals. The use of female data for the age ratio has the result of increasing the age ratio in some years, and decreasing it in others. This is probably due to sampling error.

Because of the changes in relative vulnerability during the season restricted analysis based on September wings and banding data is shown (Figures 18 through 29). The

wing survey sample is concentrated at the start of the hunting season for two reasons. More hunting takes place early in the season rather than later, and the participation rate by contributing hunters declines later in the season. Still the restriction to September reduced the sample sizes sufficiently that estimation was not possible with many of the models. Model C4ASF did not produce results for 1973 or 1974, for example.

For purposes of comparison, it is useful to display the model calculations on a time axis. Figure 30 shows the calculations of R for prairie mallards over time. The centre line on these graphs is the mean and the upper and lower lines show the 90% confidence limit for the age ratio.

The model that attempts the greatest degree of adjustment is model C4ASF. It corrects for error introduced by differential relative vulnerability among the 4 age / sex classes, corrects for identification errors among the classes, and estimates the age ratio for females only. The estimation according to model C4ASF is the most demanding of data, however, and it is of interest to see whether other models provide results consistent with those of model C4ASF, but with greater precision. Model A is of particular interest, as the model now in use by most workers, and the U.S. Fish and Wildlife Service in particular. Figures 31 and 32 compare the two models' results.

For prairie mallard data sets in years of moderate production the results of model C4ASF and model A are consistent. Therefore there seems to be little harm in using model A estimates for this species in most years. The wider confidence limits for model C4ASF may not be

of particular importance in that they derive in part from the sample used for identification error correction. The direction of bias in model A relative to model C4ASF is variable. When the age ratio is low, as in 1972, the detailed calculations of model C4ASF give a different, lower value for the age ratio with little loss in precision,

Figure 33 shows the results from September kill data from model A. These calculations give age ratios higher than those of the full data sets, in most years. (Although in 1979, for example, the September calculation is lower, suggesting that production of young near to hunting areas was so much reduced that immigration of ducks increased age ratios later in the season.) Unfortunately the restriction to September kill dates has the effect that not all estimates are precise enough to be useful. Figure 34 shows the results from model C4A, which are imprecise in 1974, 1975, 1977, and 1978.

A sex ratio analysis was also performed for prairie mallards, with data from 1979, 1980, 1981, and 1982. The results are given in Table 20.

It is encouraging to see the stability of these models for the calculation of sex ratio, which does not vary as much as age ratio, and which is expected to be from about 1 to 1.5. The low sex ratio in 1979 is associated with low production and may indicate that numbers of AM had left the region earlier than in normal years.

Table 20. Sex ratios in prairie mallards

Model	1979	1980	1981	1982
1	1.2	1.2	1.6	1.2
2	1.1	1.2	1.7	1.3
3	1.5	1.2	1.7	1.3
4	1.4	1.2	1.9	1.4
5	1.1	1.1	1.5	1.2
6	1.0	1.0	2.0	1.4
7	1.1	1.1	1.5	1.2
8	1.4	1.1	1.6	1.3
9	1.1	1.1	1.5	1.2
10	1.0	1.0	1.5	1.1
11	1.4	1.1	1.6	1.3
12	1.2	1.9	1.7	1.2
13	1.0	1.0	1.5	1.1
14	0.9	0.9	1.7	1.3

Figure 6 PRAIRIE MALLARD, 1971

Figure 7
PRAIRIE MALLARD, 1972

Figure 8 PRAIRIE MALLARD, 1973

Figure 9 PRAIRIE MALLARD, 1974

Figure 10 PRAIRIE MALLARD, 1975

Figure 11 PRAIRIE MALLARD, 1976

PRAIRIE MALLARD, 1977

Figure 12

Figure 13

PRAIRIE MALLARD, 1978

Figure 14 PRAIRIE MALLARD, 1979

Figure 15 PRAIRIE MALLARD, 1980

Figure 16 PRAIRIE MALLARD, 1981

Figure 17 PRAIRIE MALLARD, 1982

Figure 18 PRAIRIE MALLARD, SEPTEMBER, 1971

Figure 19 PRAIRIE MALLARD, SEPTEMBER, 1972

Figure 20 PRAIRIE MALLARD, SEPTEMBER, 1973

Figure 21 PRAIRIE MALLARD, SEPTEMBER, 1974

Figure 23 PRAIRIE MALLARD, SEPTEMBER, 1976

Figure 24 PRAIRIE MALLARD, SEPTEMBER, 1977

Figure 25 PRAIRIE MALLARD, SEPTEMBER, 1978

Figure 26 PRAIRIE MALLARD, SEPTEMBER, 1979

Figure 27 PRAIRIE MALLARD, SEPTEMBER, 1980

Figure 28

Figure 29 PRAIRIE MALLARD, SEPTEMBER, 1982

PRAIRIE MALLARD, MODEL R

Figure 30

PRAIRIE MALLARD, MODEL A

Figure 31

PRAIRIE MALLARD, MODEL C4ASF

Figure 32

Figure 33 PRAIRIE MALLARD, SEPTEMBER, MODEL A

Figure 34 PRAIRIE MALLARD, SEPTEMBER, MODEL C4A

2 Black Ducks from the Maritime Provinces

Figure 35 shows the unadjusted age ratios calculated for maritime province black ducks with model R. The estimates are considerably improved using the correction for relative vulnerability in model A. (Figure 36.)

This data set is well suited to analysis by the methods of this study because it deals with a relatively closed system, i.e. a system with less ingress and egress of individuals than is found in the prairies or elsewhere. All models provided estimates for all years, and the most detailed model, C4ASF, gave results that matched those of model A quite closely. Figures 37 and 38 show the results of models C4AS and C4ASF, of which C4AS is preferable because of its improved estimation in 1974 and 1976.

In some years the models behaved according to the pattern of prairie mallards, with a division between models correcting for relative vulnerability and those that do not (e.g. 1972 in Figure 39). In such years estimation according to model A may be satisfactory, as it generally is for prairie mallards.

In other years, however, other correction factors have impact on the estimation of age ratios. Figure 40 shows the model results for 1974. In this year it is primarily the models that restrict the age ratio to females that give aberrant age ratios with wide confidence limits. These were years with relatively small samples of AF wings.

The stability of estimation for maritime province black ducks indicated that the sample data might be pooled over the years of the study. This serves particularly to

show the behavior of the various models with the black duck data, as well as providing a sort of averaged estimate of the age ratio. The results are shown in table 21. (In some of the subsequent data sets the quantity of information is so limited that only this pooled analysis is shown.)

There were sufficient banding data to allow an analysis of recovery rates for maritime province black ducks. From 1971 to 1982 there were no significant pairwise (between year) differences in recovery rates for AM and AF, while for IM there were 20 and for IF there were 10 (see chapter 4).

The overall test of homogeneity of recovery rates from 1968 to 1982 had these results:

AM, $g = 27.4$ (14 df, $p < .01$) *
 AF, $g = 16.6$ (14 df, $p < .20$)
 IM, $g = 57.3$ (14 df, $p < .001$) **
 IF, $g = 46.0$ (14 df, $p < .001$) **

Recovery rates cannot be assumed to be constant. There was no indication of a difference in recovery rates between IM and IF (no significant comparisons among 15 years).

The coefficient of relative vulnerability, V , was calculated and is shown in Table 22.

As was true of prairie Mallards, V is heterogeneous among years. This heterogeneity of V was a phenomenon observed in all those data sets for which recovery rates were analysed. This implies that models that do not correct for differences in recovery rate (such as model R) do not provide reliable indices to the true age ratios.

Table 21. Age ratios from maritime black ducks 1971-1982

Model	5%	Mean	95%
R	3.35	3.65	3.95
F	3.48	3.95	4.48
A	1.18	1.34	1.50
AF	1.24	1.45	1.68
AS	1.18	1.33	1.50
ASF	1.26	1.53	1.83
C2	2.39	2.77	3.17
C2A	0.85	1.01	1.20
C4	2.18	2.64	3.12
C4F	1.33	2.23	3.24
C4A	0.77	0.97	1.17
C4AF	0.49	0.82	1.20
C4AS	0.78	0.97	1.18
C4ASF	0.50	0.86	1.28

Table 22. The coefficient of relative vulnerability for
black duck banded and recovered in the
maritime provinces

Year *	V	Standard Deviation
1970	1.68	.43
1968	1.91	.67
1974	2.00	.54
1969	2.03	.70
1971	2.10	.42
1976	2.49	.47
1980	2.55	.34
1975	2.62	1.03
1977	2.85	.45
1973	2.86	.71
1981	2.88	.71
1978	2.91	.40
1979	2.95	.48
1972	3.37	.82
1982	3.65	.78

* arranged in ascending order of V

MARITIME PROVINCES, BLACK DUCK, MODEL R

Figure 35

Figure 36. MARITIME PROVINCES, BLACK DUCK, MODEL A

Figure 37 MARITIME PROVINCES, BLACK DUCK, MODEL C4AS

Figure 38 MARITIME PROVINCES, BLACK DUCK, MODEL C4ASF

MARITIME PROVINCES, BLACK DUCK, 1972

Figure 39

Figure 40

MARITIME PROVINCES, BLACK DUCK, 1974

3 - Black ducks in Ontario and Quebec

The analysis of black duck in Ontario and Quebec was not straightforward. The most detailed model, C4ASF, did not produce results for 1977 or 1981. In fact no models produced good estimates in 1977. (Compare figure 41 for 1977 with figure 42 for 1982.)

Even model A had an unacceptably large spread of simulated results for 1977 (figure 43). For trends over the whole period either C4AF (figure 44) or C4A (figure 45) were most useful. This shows the importance of a correction of this data, based on a full (4 category) control sample.

4 - Wood duck from Ontario and Quebec

The unadjusted ratios, using model R, are shown in figure 47, except for the year 1974.

Figure 48 shows the most detailed model, C4A, with which estimation was possible for wood duck in Ontario and Quebec. The mean estimate from this model is very similar to that from model A.

In this analysis it was the models that performed recovery rate corrections based on the 4 age / sex categories that sometimes failed to give results. In 1972, for example, all models produced estimates (figure 49), while in 1975 (figure 50) and in 1977 (figure 51) none of the "AS" type models produced results. In each case this is explained by small samples in the matrix of band recoveries (only 1 AF in 1975, none in 1977). The number of invalid simulations for such data lead to the estimation program discontinuing use of the "AS" models.

Figure 41

BLACK DUCK, ONTARIO & QUEBEC, 1977

3

Figure 42 BLACK DUCK, ONTARIO & QUEBEC, 1982

Figure 43 BLACK DUCK, ONTARIO & QUEBEC, MODEL A

BLACK DUCK, ONTARIO & QUEBEC, MODEL C4AF

Figure 44

Table 23. Adjusted age ratios for the blue-winged teal
from Ontario and Quebec, 1971-1982

Model	Age Ratio	90% confidence interval
R	4.78	4.44-5.12
F	5.18	4.65-5.75
A	2.04	1.67-2.46
AF	2.21	1.77-2.69
AS	1.96	1.58-2.37
ASF	3.15	2.33-4.02
C2	5.02	3.32-7.60
C2A	2.15	1.35-3.31
C4	4.74	3.01-7.24
C4F	5.50	3.43-8.91
C4A	2.02	1.23-3.19
C4AF	2.45	1.36-4.29
C4AS	1.91	1.11-3.13
C4ASF	3.46	1.87-6.23

WOOD DUCK, ONTARIO & QUEBEC, MODEL R

Figure 46

WOOD DUCK, ONTARIO & QUEBEC, MODEL A

Figure 47

Figure 48

Figure 49

WOOD DUCK, ONTARIO & QUEBEC, 1972

Figure 50

WOOD DUCK, ONTARIO & QUEBEC, 1975

Figure 51

WOOD DUCK, ONTARIO & QUEBEC, 1977

An analysis of band recovery rates for wood duck in Ontario and Quebec is given in Chapter 4.

5 - Mallard from Ontario and Quebec

The analysis of mallard age ratios from Ontario and Quebec suggests an inadequacy in the data available for this study. Except for the low age ratio in the unadjusted result for females (model AF, figure 52), all age ratios are unusually high. To a large extent this is corrected by the adjustments made in more detailed models (eg. model C4ASF in figure 53), but the more detailed models do not allow estimation in all years. (Compare figure 54 for 1975 with figure 55 for 1982). A discussion of the difference in age ratios of mallards here with those from the prairies is given in Chapter 5.

Ontario and Quebec have seen increases in mallard population in recent years. During this period large areas of newly more important breeding habitat have not been sampled for banding. This may contribute to the weakness of these models for the analysis of age ratios, in that the banding sample used for correction may not adequately represent the birds shot. The increase in mallards here is discussed in more detail in Chapter 7, in comparison with the sympatric near relative, the black duck.

6 - Blue-winged teal from Ontario and Quebec

Data were combined for all years for the analysis of Ontario and Quebec blue-winged teal. The results of this analysis are shown in Table 23.

Table 23. Adjusted age ratios for the blue-winged teal
from Ontario and Quebec, 1971-1982

Model	Age Ratio	90% confidence interval
R	4.78	4.44-5.12
F	5.18	4.65-5.75
A	2.04	1.67-2.46
AF	2.21	1.77-2.69
AS	1.96	1.58-2.37
ASF	3.15	2.33-4.02
C2	5.02	3.32-7.60
C2A	2.15	1.35-3.31
C4	4.74	3.01-7.24
C4F	5.50	3.43-8.91
C4A	2.02	1.23-3.19
C4AF	2.45	1.36-4.29
C4AS	1.91	1.11-3.13
C4ASF	3.46	1.87-6.23

Banding recoveries from blue-winged teal banded in Ontario and Quebec were too few to allow a more detailed analysis. Overall tests for homogeneity of recovery rates showed the usual pattern of heterogeneity among years for immatures:

AM g = 12.64 (12 df, .4 > p > .3)

AF g = 17.86 (13 df, .2 > p > .1)

IM g = 46.28 (14 df, p << .001) **

IF g = 52.74 (14 df, p << .001) **

MALLARD, ONTARIO & QUEBEC, MODEL C4ASF

Figure 53

* missing values interpolated

Figure 54

MALLARD, ONTARIO & QUEBEC, 1975

Figure 55
MALLARD, ONTARIO & QUEBEC, 1982

7 - Pintail in the prairie provinces

Figure 56 shows the estimates of age ratio, with 90% confidence limits for pintail shot in the prairie provinces from 1971 to 1982, using model C4ASF.

As with mallards in the prairies the models that do not correct on the basis of banding give results very different from those that are corrected. Model C4ASF generally gives results higher than model C4AS, showing the importance of superfluous AM in the wing sample. The 14 models all give different results for pintail, establishing the need for complete corrections when possible. Model C4AF and model C4ASF are sufficiently different, for example, to suggest that banding corrections based on all 4 age / sex categories should be used. The estimates of pintail age ratios under this model are shown in Table 24.

The estimates vary much more than those for mallard and have wider confidence limits, but this may be primarily a reflection of sample size. Otherwise there are several important differences in the indices for pintail and mallard. Pintail are known to have a breeding strategy adapted to variable habitat conditions (Smith 1970), readily shifting the breeding area north in dry years and generally displaying greater mobility and flexibility than other Anas species (Derrickson 1978). The different strategy may explain the opposing tendencies in pintail and mallard. In fact the graph for pintail age ratios increases when the mallard decreases, and vice versa, in 9 out of the 11 year to year changes involved.

A recovery rate analysis was performed. The small number of recoveries did not allow a powerful test of

Table 24. Estimates of age ratio for pintail in the prairie provinces using model C4ASF

Year	5%	Mean	95%
1971	1.27	2.33	3.88
1972	0.60	1.09	1.75
1973	1.81	3.73	6.86
1974	0.30	0.80	1.57
1975	0.65	1.51	2.80
1976	1.02	2.37	4.78
1977	0.33	0.87	1.80
1978	0.49	1.19	2.28
1979	0.79	1.55	2.66
1980	0.18	0.47	0.91
1981	0.63	1.39	2.65
1982	0.57	1.52	3.17

Table 25. Relative vulnerability V from pintails banded and recovered in the prairie provinces

Year	V	Standard Deviation
1975	1.84	0.58
1981	2.30	2.00
1980	2.47	1.61
1973	2.50	1.13
1978	2.67	1.45
1974	2.68	1.26
1982	3.24	1.86
1976	3.30	1.28
1970	3.39	1.31
1968	3.75	1.64
1969	4.25	2.23
1979	4.45	2.34
1972	4.84	2.99
1977	5.49	3.54
1971	5.56	3.42

PINTAIL PRAIRIE, MODEL C4ASF

Figure 56

homogeneity among years, but the range of relative vulnerabilities among years, shown in Table 25, shows the usual pattern of heterogeneity.

8 - Blue-winged teal from the prairie provinces

As for the Ontario-Quebec data, all years 1971-1982 were combined for analysis of blue-winged teal age ratios from the prairie provinces.

The results of calculation are shown in Table 26.

9 - Gadwall from the prairie provinces

Gadwall data, combined for the years 1971-1982, produced the age ratio estimates shown in Table 27.

Control samples were not adequate to allow the use of more detailed models.

10 - American wigeon from the prairie provinces

American wigeon data, combined for the years 1971-1982, gave the results shown in Table 28.

Banding and control sample data were insufficient for further estimation.

11 - Bufflehead from throughout Canada

Bufflehead data, combined for the years 1971-1982, gave the results shown in Table 29.

Table 26. Adjusted age ratios for blue-winged teal from the prairie provinces, 1971-1982

Model	Age Ratio	90% confidence interval
R	6.89	5.95-7.95
F	4.37	3.66-5.19
A	1.09	0.76-1.51
AF	0.69	0.47-0.95
AS	1.28	0.85-1.78
ASF	1.18	0.73-1.69
C2	(NO ESTIMATE)	
C2A	1.57	0.75-3.18
C4	(NO ESTIMATE)	
C4F	4.54	2.77-7.12
C4A	1.66	0.77-3.43
C4AF	0.75	0.39-1.23
C4AS	2.60	0.91-6.82
C4ASF	1.27	0.61-2.27

Table 27. Adjusted age ratios for gadwall from the prairie provinces, 1971-1982

Model	Age Ratio	90% confidence interval
R	2.41	2.14-2.72
F	3.48	2.87-4.20
A	0.99	0.51-1.61
AF	1.44	0.72-2.36
AS	1.05	0.42-1.86
ASF	1.87	-0.60-3.58
C2	1.27	1.09-1.48
C2A	0.53	0.27-0.86

Table 28. Adjusted age ratios for American wigeon from the prairie provinces, 1971-1982.

Model	Age Ratio	90% confidence interval
R	4.56	3.90-5.31
F	4.41	3.56-5.34

Table 29. Adjusted age ratios for bufflehead from throughout Canada, 1971-1982.

Model	Age Ratio	90% confidence interval
R	1.36	1.29-1.44
F	2.20	2.00-2.40

12 - Hooded merganser from throughout Canada

Hooded merganser data, combined for all of Canada and for the years 1971-1982 gave the results shown in Table 30.

In Table 30 results from models C2A and A are the same because the control sample had no age identification errors. The same is true for C2 and R. The preferred models are A and C2A, which provide a more acceptable estimate than do models without the relative vulnerability adjustment.

13 - Redhead from throughout Canada

An analysis of Redhead data, combined for all of Canada, and for the years 1971-1982 produced the results in Table 31.

14 - Lesser scaup from throughout Canada

Lesser scaup data, combined for all of Canada and for the years 1971-1982 gave the results shown in Table 32.

15 - Ring-necked Duck from throughout Canada

Ring-necked Duck data, combined for all of Canada and for the years 1971-1982 gave the results shown in Table 33.

16 - Canvasback from throughout Canada

Canvasback data, combined for all of Canada and for the years 1971-1982 gave the results shown in Table 34.

Table 30. Adjusted age ratios for Hooded Merganser from throughout Canada, 1971-1982

Model	Age Ratio	90% confidence interval
R	0.33	0.29-0.38
F	0.24	0.18-0.31
A	1.33	0.40-2.87
AF	0.97	0.28-2.22
C2	0.33	0.29-0.38
C2A	1.33	0.40-2.87

Table 31. Adjusted age ratios for Redhead from throughout Canada, 1971-1982

Model	Age Ratio	90% confidence interval
R	2.78	2.60-2.97
F	3.22	2.90-3.56
A	5.76	5.05-6.49
AF	6.66	5.70-7.64
AS	5.74	5.00-6.53
ASF	5.22	4.22-6.34
C2	2.78	2.60-2.97
C2A	5.76	5.05-6.49

Table 32. Adjusted age ratios for Lesser Scaup from throughout Canada, 1971-1982

Model	Age Ratio	90% confidence interval
R	2.89	2.76-3.02
F	3.08	2.89-3.28
C2	3.38	2.06-5.62
C4	3.38	2.03-5.67

17 - Green-winged teal from the prairie provinces

There were sufficient data for prairie provinces green-winged teal to allow estimation of results in most years, but without sufficient quality to allow the graphic display used earlier. Instead the results are displayed in tabular form, in Table 35.

In both 1974 and 1978 the program rejected all models for this Green-winged Teal data. Table 36 gives the "central values" for the models for those years.

Table 33. Adjusted age ratios for Ring-necked Duck from throughout Canada, 1971-1982

Model	Age ratio	90% confidence interval
R	3.22	3.07-3.37
F	3.35	3.14-3.57
A	3.98	3.27-4.77
AF	4.15	3.37-4.99
AS	3.81	3.06-4.67
ASF	3.41	2.42-4.52
C2	2.95	0.41-7.62
C2A	3.58	0.51-9.03

Table 34. Adjusted age ratios for canvasback from throughout Canada, 1971-1982

Model	Age ratio	90% confidence interval
R	3.34	3.03-3.67
F	3.42	2.95-3.94
A	7.17	6.02-8.50
AF	7.35	5.93-8.87
AS	5.81	4.57-7.11
ASF	3.71	2.68-4.87
C2	1.59	0.65-2.72
C2A	3.41	1.39-6.22

Table 35. Adjusted age ratios for green-winged teal from the prairie provinces (± standard deviation of estimate)

Model	1971	1972	1973	1975	1976
R	7.20 <u>+1.57</u>	2.88 <u>+0.61</u>	6.17 <u>+1.74</u>	6.04 <u>+2.32</u>	5.06 <u>+1.73</u>
F	7.39 <u>+1.75</u>	1.92 <u>+0.56</u>	5.14 <u>+2.04</u>	-	4.74 <u>+1.85</u>
A	5.76 <u>+2.38</u>	2.46 <u>+1.14</u>	5.29 <u>+2.39</u>	5.04 <u>+2.53</u>	4.32 <u>+2.10</u>
AF	5.93 <u>+2.47</u>	1.64 <u>+0.86</u>	4.39 <u>+2.34</u>	-	4.07 <u>+2.15</u>
AS	5.71 <u>+2.51</u>	3.31 <u>+1.90</u>	-	-	4.85 <u>+2.52</u>
ASF	5.48 <u>+2.69</u>	1.57 <u>+1.02</u>	4.06 <u>+2.41</u>	-	3.78 <u>+2.19</u>
C2	-	2.92 <u>+1.09</u>	-	-	-
C2A	-	2.50 <u>+1.42</u>	-	-	4.95 <u>+2.52</u>
C4	6.81 <u>+2.10</u>	2.70 <u>+1.06</u>	-	-	4.96 <u>+2.17</u>
C4F	6.08 <u>+2.14</u>	1.13 <u>+0.56</u>	3.94 <u>+2.14</u>	-	3.65 <u>+1.90</u>
C4A	5.54 <u>+2.49</u>	2.32 <u>+1.35</u>	-	-	4.32 <u>+2.40</u>
C4AF	4.99 <u>+2.44</u>	0.97 <u>+0.67</u>	3.42 <u>+2.22</u>	-	3.17 <u>+2.06</u>
C4AS	-	3.68 <u>+2.36</u>	-	-	-
C4ASF	4.60 <u>+2.57</u>	0.94 <u>+0.77</u>	3.22 <u>+2.29</u>	-	2.95 <u>+2.05</u>

Table 35. (contd.) Adjusted age ratios for green-winged teal from the prairie provinces (+ standard deviation of estimate)

Model	1977	1979	1980	1981	1982
R	-	5.81 <u>+2.29</u>	4.15 <u>+1.65</u>	6.56 <u>+2.20</u>	-
F	6.54 <u>+2.23</u>	-	3.31 <u>+1.53</u>	5.41 <u>+2.14</u>	5.17 <u>+3.00</u>
A	6.14 <u>+2.56</u>	-	3.54 <u>+1.95</u>	5.36 <u>+2.45</u>	-
AF	5.51 <u>+2.54</u>	4.90 <u>+2.58</u>	2.83 <u>+1.71</u>	4.63 <u>+2.50</u>	-
AS	-	-	4.27 <u>+2.44</u>	-	-
ASF	5.15 <u>+2.76</u>	4.56 <u>+2.64</u>	2.70 <u>+1.93</u>	4.35 <u>+2.58</u>	-
C2	-	-	4.48 <u>+2.18</u>	-	-
C2A	-	-	3.83 <u>+2.37</u>	-	-
C4	-	-	3.50 <u>+1.93</u>	-	-
C4F	-	4.55 <u>+2.43</u>	2.39 <u>+1.62</u>	4.21 <u>+2.22</u>	-
C4A	-	-	3.01 <u>+2.04</u>	-	-
C4AF	4.65 <u>+2.60</u>	3.91 <u>+2.55</u>	2.05 <u>+1.63</u>	3.61 <u>+2.33</u>	-
C4AS	-	-	3.88 <u>+2.55</u>	-	-
C4ASF	4.36 <u>+2.73</u>	3.71 <u>+2.65</u>	1.93 <u>+1.69</u>	3.49 <u>+2.47</u>	-

Table 36. Central values of adjusted age ratios for green-winged teal from the prairie provinces for years in which all models were rejected

Model	1974	1978
R	6.75	8.75
F	6.00	8.00
A	5.48	7.10
AF	4.87	6.49
AS	6.45	8.54
ASF	4.57	6.10
C2	11.13	-
C2A	9.03	-
C4	6.79	-
C4F	4.72	7.16
C4A	5.51	-
C4AF	3.83	5.81
C4AS	7.89	-
C4ASF	3.60	5.46

Comparison of age ratio results with $R_{critical}$

Both in the calculation of $\hat{R}_{critical}$ from banding data and in the estimation of age ratios the scope of this study has been limited by availability of data. Among the possible comparisons that might have been made only 13 data sets remain. In some cases this requires the use of a larger region for the banding data than for the wing sample, or the use of an average value for $R_{critical}$.

Table 37 shows the comparison of $\hat{R}_{critical}$ to estimated age ratios for the species and years in which estimates are available. As a measure of the difference between the measured and critical values an approximately normally distributed index was calculated:

$$Z^2 = \frac{(\hat{R} - \hat{R}_{critical})^2}{(\hat{s.e.}(\hat{R}))^2 + (\hat{s.e.}(\hat{R}_{critical}))^2} \quad (31)$$

If there were no difference between the two values for R (as parameters) in Table 37, and if the sample sizes were sufficiently large, Z would be normally distributed with mean 0 and variance 1. Z therefore measures the departure of R from the estimated critical value, relative to the precision of estimation.

Table 37 Comparison of adjusted age ratios to the theoretical age ratio, $\hat{R}_{critical}$, calculated from survival rates estimated from band recoveries

Species	Region	Year	Model	$\hat{R}_{+s.e.}$	$\hat{R}_{critical+ s.e.}$	$\hat{Z}$
Mallard	Prairie	71	C4AS	.70 $\pm$.18	.788 $\pm$.085	0.44
		72		.35 $\pm$.17	.946 $\pm$.097	3.05
		73		.55 $\pm$.22	.652 $\pm$.080	0.44
		74		.76 $\pm$.23	.575 $\pm$.081	0.76
		75		.94 $\pm$.23	.435 $\pm$.050	1.50
		76		.89 $\pm$.18	.804 $\pm$.056	0.46
		77		.85 $\pm$.18	.534 $\pm$.057	1.67
		78		.88 $\pm$.18	.638 $\pm$.056	1.28
		79		.63 $\pm$.16	.500 $\pm$.049	0.78
		80		.73 $\pm$.20	.922 $\pm$.076	-0.90
Black duck	Maritimes	71	C4AS	1.27 $\pm$.35	.644 $\pm$.297	1.36
		72		.35 $\pm$.12	.984 $\pm$.257	1.68
		73		.77 $\pm$.30	1.416 $\pm$.383	1.33
		74		1.33 $\pm$.56	1.137 $\pm$.523	0.25
		75		.89 $\pm$.42	.565 $\pm$.410	0.55
		76		2.04 $\pm$.68	1.345 $\pm$.381	0.89
		77		.97 $\pm$.31	1.055 $\pm$.214	0.23
		78		1.05 $\pm$.28	1.005 $\pm$.230	0.12
		79		1.27 $\pm$.44	.406 $\pm$.157	1.85
		80		1.27 $\pm$.36	.572 $\pm$.279	1.53

Table 37 (contd.) Comparison of adjusted age ratios to the theoretical age ratio, $\hat{R}$ critical¹ calculated from survival rates estimated from band recoveries

Species	Region	Year	Model	$\hat{R} \pm s.e.$	$\hat{R}_{critical} \pm s.e.$	$\hat{Z}$
Mallard	Ontario- Quebec	71	C4A	3.94 $\pm$ 1.00	.686 $\pm$.118	3.23
		72		.06 $\pm$ 0.03	.686 $\pm$.118	5.14
		73		7.32 $\pm$ 1.88	.686 $\pm$.118	3.52
		74		4.09 $\pm$ 0.82	.686 $\pm$.118	4.11
		76		2.56 $\pm$ 0.69	.686 $\pm$.118	2.68
		77		3.76 $\pm$ 1.12	.686 $\pm$.118	2.73
		78		5.68 $\pm$ 2.02	.686 $\pm$.118	2.47
		79		3.41 $\pm$ 0.97	.686 $\pm$.118	2.79
		80		4.89 $\pm$ 1.21	.686 $\pm$.118	3.46
Blue-winged teal	Ontario- Quebec	71	C4AS	1.91 $\pm$ 0.64	1.261 $\pm$.231	0.95
		72		1.91 $\pm$ 0.64	.769 $\pm$.206	1.70
		73		1.91 $\pm$ 0.64	.567 $\pm$.189	2.01
		74		1.91 $\pm$ 0.64	.872 $\pm$.219	1.53
		75		1.91 $\pm$ 0.64	.617 $\pm$.171	1.95
		76		1.91 $\pm$ 0.64	.821 $\pm$.161	1.65
		77		1.91 $\pm$ 0.64	.825 $\pm$.210	1.61
		78		1.91 $\pm$ 0.64	.483 $\pm$.154	2.17
		79		1.91 $\pm$ 0.64	.733 $\pm$.162	1.78
		80		1.91 $\pm$ 0.64	1.355 $\pm$.337	0.77

Table 37 (contd.) Comparison of adjusted age ratios to the theoretical age ratio, $\hat{R}_{critical}$ calculated from survival rates estimated from band recoveries

Species	Region	Year	Model	$\hat{R} \pm s.e.$	$\hat{R}_{critical} \pm s.e.$	$\hat{Z}$
Black duck	Ontario- Quebec	71	C4A	2.17 $\pm$ 0.44	.678 $\pm$.240	2.98
		72		.66 $\pm$ 0.17	.678 $\pm$.240	0.06
		73		1.88 $\pm$ 0.57	.678 $\pm$.240	1.94
		74		2.73 $\pm$ 0.67	.678 $\pm$.240	2.88
		75		2.13 $\pm$ 0.70	.678 $\pm$.240	1.96
		76		2.88 $\pm$ 0.86	.678 $\pm$.240	2.47
		77		3.83 $\pm$ 1.50	.678 $\pm$.240	2.07
		78		2.25 $\pm$ 0.75	.678 $\pm$.240	2.00
		79		1.95 $\pm$ 0.80	.678 $\pm$.240	1.52
		80		2.32 $\pm$ 0.85	.678 $\pm$.240	1.86
Wood duck	Ontario- Quebec	71	C4A	3.69 $\pm$ 2.01	1.087 $\pm$.399	1.27
		72		.94 $\pm$ 0.37	2.276 $\pm$.756	1.59
		73		1.43 $\pm$ 0.97	1.268 $\pm$.570	0.13
		74		1.05 $\pm$ 0.71	1.427 $\pm$.571	0.41
		75		1.10 $\pm$ 0.64	.870 $\pm$.400	0.30
		76		2.03 $\pm$ 1.10	.736 $\pm$.302	1.13
		77		.31 $\pm$ 0.17	1.856 $\pm$.590	2.52
		78		1.36 $\pm$ 0.73	1.622 $\pm$.671	0.26
		79		3.48 $\pm$ 2.78	1.379 $\pm$.817	0.73
		80		1.61 $\pm$ 0.87	1.366 $\pm$.838	0.20

Table 37 (contd.) Comparison of adjusted age ratios to the theoretical age ratio, $\hat{R}_{critical}$ calculated from survival rates estimated from band recoveries

Species	Region	Year	Model	$\hat{R} \pm s.e.$	$\hat{R}_{critical} \pm s.e.$	$\hat{Z}$
Pintail	Prairies	71	C4AS	.85 $\pm$ 0.29	.711 $\pm$.179	0.41
		72		.91 $\pm$ 0.29	.546 $\pm$.166	1.09
		73		1.97 $\pm$ 0.75	.396 $\pm$.222	2.01
		74		.69 $\pm$ 0.30	.579 $\pm$.175	0.32
		75		1.35 $\pm$ 0.60	.502 $\pm$.139	1.38
		76		1.50 $\pm$ 0.68	.525 $\pm$.120	1.41
		77		.42 $\pm$ 0.19	.310 $\pm$.128	0.48
		78		.96 $\pm$ 0.40	.661 $\pm$.184	0.68
		79		.94 $\pm$ 0.33	.578 $\pm$.203	0.93
		80		.25 $\pm$ 0.13	.127 $\pm$.162	0.59
Blue-winged teal	Prairies	71	C4AS	2.60 $\pm$ 1.92	1.261 $\pm$.231	0.69
		72		2.60 $\pm$ 1.92	.769 $\pm$.206	0.95
		73		2.60 $\pm$ 1.92	.567 $\pm$.189	1.05
		74		2.60 $\pm$ 1.92	.872 $\pm$.219	0.89
		75		2.60 $\pm$ 1.92	.617 $\pm$.171	1.03
		76		2.60 $\pm$ 1.92	.821 $\pm$.161	0.92
		77		2.60 $\pm$ 1.92	.825 $\pm$.210	0.92
		78		2.60 $\pm$ 1.92	.483 $\pm$.154	1.10
		79		2.60 $\pm$ 1.92	.733 $\pm$.162	0.97
		80		2.60 $\pm$ 1.92	1.355 $\pm$.337	0.64
Gadwall	Prairies	all	AS	1.05 $\pm$ 0.43	1.245 $\pm$.407	-0.33
American widgeon	Prairies	all	R	4.56 $\pm$ 0.42	.791 $\pm$.103	8.72

Table 37 (contd.) Comparison of adjusted age ratios to the theoretical age ratio, $\hat{R}_{critical}$ calculated from survival rates estimated from band recoveries

Species	Region	Year	Model	$\hat{R} \pm s.e.$	$\hat{R}_{critical} \pm s.e.$	$\hat{Z}$
Green-winged teal	Prairies	71	C4A	5.54 $\pm$ 2.49	1.396 $\pm$.383	1.64
		72	C4A	2.32 $\pm$ 1.35	2.211 $\pm$.508	0.08
		73	A	5.29 $\pm$ 2.39	1.058 $\pm$.585	1.72
		75	A	5.04 $\pm$ 2.53	.420 $\pm$.309	1.81
		76	C4A	4.32 $\pm$ 2.40	1.784 $\pm$.402	1.04
		77	A	6.14 $\pm$ 2.56	.705 $\pm$.321	2.11
		79	R	5.81 $\pm$ 2.29	1.291 $\pm$.502	1.93
		80	C4A	3.01 $\pm$ 2.04	1.185 $\pm$.635	0.85
Redhead	Canada	all	C2A	5.76 $\pm$ 0.43	1.185 $\pm$.140	0.12
Lesser scaup	Canada	all	C4	3.38 $\pm$ 1.29	.853 $\pm$.194	1.94

7 - DISCUSSION

The age ratios in the last chapter come from over 200,000 duck wings that were examined during the years 1971-82. In this chapter the results are considered in the spirit of Chapter 1. Is there sufficient information remaining after correction to allow inferences to be made about duck population changes, on the basis of these age ratios? Can these experimental results tell us something about the applicability of theoretical ecology to wild North American ducks? How can the future use of these surveys be improved?

The discussion is divided into five sections. In the first section, Putting Age Ratios into Perspective, the results are examined in relation to other sources of biological information. For the prairies, annual population counts and productivity indices are available from the aerial survey program. These are compared with age ratios from this study. It must be remembered that the aerial survey results may be subject to important errors that vary year-to-year. These errors can not be considered in the scope of this study. The discussion is therefore subjective, dealing with the estimates themselves and not their associated confidence regions. A discussion of how the estimated age ratios compare to $\hat{R}$ is also given in this section.
critical

In the second section, Trends in Population, the results are reviewed to show what they imply for some species' population changes during the study period. An attempt is made to explain the observed age ratios. The experimental details of this study were directed at measurement of age ratios and do not bring direct evidence on questions of cause and effect. (For reasons

why this more detailed approach was not feasible in the case of climatic variation, see Chapter 3.) Still, some likely or major causes of change are evident, and are discussed here.

In the third section, Global Population Dynamics of Ducks, some possible methods of study are investigated for their applicability. For maritime black ducks, Leslie matrix theory can be used to find out what sort of stable age distribution could result from the age ratios found in this study. Unfortunately, most of the duck data sets have strong departures from the prerequisites needed to give stable age distributions according to this theory. The other main approaches currently in use to study duck population dynamics globally draw primarily on bird band recoveries. These approaches have so far failed to find strong links between hunting regulations and duck populations. Some directions for further analysis are proposed.

In the fourth section age ratios from 24 species of duck are compared. The age ratio is shown to vary inversely with the size of the bird. Does this fact have evolutionary significance?

Finally, a section of suggested improvements that could be made to give more power to the methods of this study are given.

Putting Age Ratios into Perspective

At the end of Chapter 3 some local studies were reviewed that provided information that could be used to validate the age ratios obtained in this study. These studies were, however, limited in scope, and did not account for non-breeding birds.

Theoretically, the annual aerial surveys of prairie populations and production could be used to validate the age ratios more directly, in that region. Unfortunately the aerial surveys themselves have important sources of error, especially related to species other than mallard and to counts of duck broods.

It is not possible to give here a thorough review of the sources of error in the aerial surveys. This is the subject of an ongoing review by the U.S. Fish and Wildlife Service, from which no published results are yet available. Some errors in the May population surveys derive from identification, visibility, and counting (errors which vary for different observers), survey timing (some birds are migrating as the survey is going on and so might be subject to enumeration more than once, or not at all), and the determination of transect width. In the July production surveys the difficulty of observation is more severe, and it is not possible to identify the species of birds seen in broods. The indices from the production survey are not directly comparable to age ratios. Appendix 6 shows how the July survey results were combined with those of the May survey to give an index to production that should be proportional to age ratios. In the graphs discussed below the index was multiplied by a scale factor to facilitate comparison with age ratios.

Figure 57 demonstrates the close pattern of change comparison between the production index calculated from the July aerial surveys, and the wing survey result, R (with model C4AS) for the prairie pintail. The two graphs agree, for example, on peaks in 1973, 1976, and 1978, and on lows in 1977 and 1980. The pattern comparison between the same index from the July surveys with this study's results for the green-winged teal (figure 58) shows even closer apparent agreement, but the models used (see Table 37) did not produce results for 1974 or 1978 and these were interpolated in the graph.

For the mallard, the only other species from the prairies for which a comparison was attempted, the situation is much less clear. Both indices agreed on relatively good production in 1978 and poor in 1972 (figure 59), but showed little further similarity. Some parts of the pattern were better matched by limiting the aerial survey results, for example to southern Manitoba (figure 60), but then the erratic behavior of results from smaller samples predominates.

The aerial production surveys do not identify species. Where population counts are available it is possible to examine more directly the trend induced by certain levels of production. In figure 61 are shown $\hat{R}$ (from model C4AS), and $\hat{R}_{critical}$ for the prairie mallard. For comparison (from U.S. / Canada cooperative surveys) population levels for the mallard in the prairies are shown in figure 62. There are three time periods for mallards. In 1971-1973 $\hat{R}$ is less than $\hat{R}_{critical}$ and so population in the following years should decrease. The same is true in 1980. From 1974 to 1979 $\hat{R}$ is greater than $\hat{R}_{critical}$ so there is potential for increase. In

FIGURE 57 COMPARISON OF INDICES OF PRODUCTION FROM AERIAL SURVEYS (---) AND WING SURVEY (—) FOR THE PINTAIL IN THE PRAIRIES.

FIGURE 53 COMPARISON OF INDICES OF PRODUCTION FROM AERIAL
SURVEYS (—•—) AND WING SURVEY (——) FOR THE
GREEN-WINGED TEAL IN THE PRAIRIES.

FIGURE 59 COMPARISON OF INDICES OF PRODUCTION FROM AERIAL SURVEYS* (— · —) AND WING SURVEY (——) FOR THE MALLARD IN THE PRAIRIES.

FIGURE 60 COMPARISON OF INDEX OF PRODUCTION FROM AERIAL SURVEYS
IN SOUTHERN MANITOBA (— · — · —) WITH THE WING SURVEY
AGE RATIO FOR PRAIRIE MALLARDS (——).

FIGURE 61 COMPARISON OF R CRITICAL (— · — · —) AND R (—) FOR THE PRAIRIE PROVINCE MALLARD.

FIGURE 62 POPULATION OF THE PRAIRIE MALLARD, ESTIMATED BY MAY
AERIAL SURVEYS.

fact the population did decrease markedly from 1972 to 1974, and again from 1980 to 1981. From 1975 to 1980 the changes are much less, although the 3 large excesses of $\hat{R}$ over $\hat{R}_{critical}$ are matched by annual increases in two years. As is discussed in the next section with regard to black duck displacement from breeding habitat (for example by agricultural encroachment) may prevent regional population increase even when $\hat{R}$ is greater than $\hat{R}_{critical}$.

In most other areas of the country broad-scale aerial surveys are not used. Then an indirect indicator of population that could be used is the total kill of a species by hunters, as estimated by the national surveys of duck kill. Figure 63 presents a comparison using this source for Ontario and Quebec wood ducks. As for figures 61 and 62 we are interested in the change in the population index (this time the kill) in the years following those when $\hat{R}$ is greater than $\hat{R}_{critical}$. Based on the magnitude of this difference relative to the error of measurement (i.e., based on $\hat{Z}$ in Table 37), we would expect increases in population following 1971 and 1976, and decreases following 1972 and 1977. Other values of $\hat{Z}$ in Table 37 are not great enough in magnitude to predict change. Figure 63 shows a slight increase in kill in 1972, an increase in 1977, a decrease in 1973, but an increase in 1978. In 1979 an increase is predicted (for 1980) with weak significance. This change is observed. For other years the magnitude of $\hat{Z}$ is too small to allow prediction. Considering the crude index to population provided by hunter kill estimates, $\hat{Z}$ provides a reasonable prediction of change.

Equation 8 establishes the link between age ratios and survival rates for ducks that breed at one year of age.

FIGURE 63 KILL (—○—) OF WOOD DUCK IN ONTARIO AND QUEBEC,
WITH R (—●—) AND R CRITICAL (—○—).

If R , S_A , and S_I could be measured without error then that equation would determine whether the population increases or decreases over the period of one year. The simple form of this equation comes from the reduction into two categories, immatures (the current year's production, which is non-breeding, and of which all survivors will be recruited into the next year's breeding population), and adults (breeders, not subdivided into age classes).

The utility of age ratios is not determined by the theoretical possibility of use, but by the practical determination of the necessary statistics with sufficient accuracy to allow hypothesis testing. From this point of view Table 37 summarizes the results of this study succinctly. If it is true:

- 1 - that the adjustment of age ratios has been sufficient to reduce bias to an acceptable level, and survival rates are representative of the same population, and unbiased, and
- 2 - that the population level is stable for the period of one year (to give a zero mean to Z)

then $\hat{Z}$ in Table 37 will have the normal distribution, with mean 0 and variance 1. (Allowing the usual requirements for the t-test, and approximation of t by the normal distribution).

In most cases it is not likely that any of these populations has had a consistent increase over the period of this study, with the possible exception of the Mallard in Ontario and Quebec. Data such as those for the blue-winged teal from Ontario and Quebec (which has

all values of $\hat{Z}$ near 1, or clearly greater than 1) indicates a relative bias between R and $R_{critical}$ that has not been removed by the corrections applied. To some extent this direction of bias is common to all data sets examined, in varying degrees. The effect of the lingering bias is to increase R , or to decrease $R_{critical}$, or both. (A similar result was found by Martin et al., 1979, in their check of consistency of duck population parameters.)

The extent of the problem of large "Z" values varies among the data sets examined. Because it occurs to some degree with all data sets, regardless of the models used for correction, it is likely that there is a consistent bias in the determination of $R_{critical}$.

The banding analyses give survival estimates that could be too high. Nichols et al. (1982) found that a zero or positive correlation between survival and recovery rates from banding of disjoint subgroups lead to a positive bias in the survival estimates from one of the models used in this study. (Model H1.) The results depended on heterogeneity in the population of birds banded. They suggested that the bias would be stronger in winter-banded birds, however the recoveries in this study are from preseason bandings.

Pollock and Ravelling (1982) also considered bias in survival estimators caused by heterogeneity. They concluded that heterogenous survival rates among individuals would probably lead to a negative bias in the estimation of survival, although positive bias (as is suggested in this study) could occur if the population segments differed mostly in natural, rather than hunting mortality.

The sampling method in the wing survey may also cause a shift in the values of $\hat{Z}$. Appendix 8 shows that, by ignoring cluster-based analysis in the survey, R may be overestimated.

In other cases, those for which the mean value of $\hat{Z}$ are large, either the correction model was too limited, or, for those models that used the "A" or "AS" corrections, the needed banding data were too limited to be representative of the population of birds that was sampled in the wing collection.

If the non-zero mean of $\hat{Z}$ is ignored, (as by acceptance of hypothesis 1, above) then $\hat{Z}$ becomes an index to population change. On some range, say $(-1.96 < \hat{Z} < 1.96)$ for 5% significance with a two-tailed test, $\hat{Z}$ would indicate no detectable change in population, while larger absolute values of $\hat{Z}$ indicate significant change.

If a bias is apparent (but it is assumed that there has been no long term trend in population), then extreme values of $\hat{Z}$ indicate change in population status if those factors that are not controlled by the correction methods have constant effect. In this case $\hat{Z}$ can be compared to the mean of $\hat{Z}$ over the study period.

Even if $\hat{Z}$ cannot be calculated, as is the case when usable estimates of survival are not available, one may still assume that uncontrolled factors have constant effect, and use the age ratios produced in this study as indices of change. Unless only very large changes in the index are considered it would be unwise to use the models without "A" or "AS" correction to make the index. This is because all banding data sets analysed in this report have had recovery rates and relative

vulnerability that vary among years.

With these guiding principles the results in Table 37 can be reviewed. The next section includes this review in species accounts.

Trends in Population

In the previous section it was shown that age ratios calculated in this study matched other available population information where it was available. In this section a comparison of R and $R_{critical}$ is used for several species to indicate the inferences that can be made about population change.

1. Mallard in the prairie provinces. This group provides a set of values for $\hat{Z}$ that is reasonably well distributed, with both negative and positive values. The relative bias between $\hat{R}$ and $\hat{R}_{critical}$ can be ignored, as a first approximation. At a 10% level of significance, the results indicate a shortfall in recruitment in 1972, and a surplus in 1977. Population estimates for this group are available from aerial surveys, and are discussed in the previous section. Of interest here is that those surveys do not show a decline in 1978. 1977 was a poor year for duck breeding in the southern prairies (see pond counts Table 6). This was followed by poor conditions for hunting (see Table 7). Perhaps because hunting kill was low the survival rates of adults (71.5%) and young (53.4%) were good. The resulting low value of $R_{critical}$ that year was the main reason for the (marginally) significant $\hat{Z}$. If there is a small relative bias that results in a positive mean for $\hat{Z}$, the value in 1977 would not be significant.

Three possible interpretations for the disagreement regarding the change from 1977 to 1978 found in this study and in the aerial surveys, then, are that a type I error occurred in the aerial surveys, that the aerial surveys were wrong and there was surplus production in 1977, or that the limitations of this study involve a

non-zero mean of $\hat{Z}$ that gives false significance to small positive values of $\hat{Z}$.

If a decrease of 0.5 is accepted for $\hat{Z}$ in this data set's interpretation, then 4 out of 10 years have absolute value of $\hat{Z}$ greater than 1. (1972, 1975, 1977, and 1980). The problem with 1978 remains, but this method otherwise provides a good match with the population changes in figure 61.

2. Black Duck in the maritimes. As for the prairie mallard we might accept that Z has a distribution that approximates the standard normal. Ignoring a shift of Z values, then, at 10% significance, the results indicate a decrease in population from 1972 to 1973 and an increase from 1979 to 1980.

There is no estimate of breeding populations for black ducks, and wintering counts are notoriously difficult to interpret. In eastern Canada, mallards, black ducks, and wood duck also have low age ratios relative to R in 1972, suggesting a general effect. That year had the coldest summer months in eastern Canada in 40 years (see Table 7 and accompanying discussion). Other studies have indicated poor duck production then (e.g. Reed, 1975).

Overall the stability of the black duck population in the maritimes seems remarkable among the data sets studied. This allowed an attempt to determine a stable age distribution, which is described in the next section.

3. Mallard and black duck in Ontario and Quebec.

Mallard and black duck are closely related species with

similar behavior and migration patterns in Ontario. During the period of this study changes were evident in the relative numbers of these species, especially in southern Ontario (D. Dennis, who has surveyed parts of southern Ontario for breeding waterfowl, provided this unpublished information.) In Quebec away from the Ontario border region the black duck has been and remains the more numerous of the two species, but the mallard is increasing there, as well. (D. Dennis, pers. comm.)

While there may be an error in the estimation of $R_{critical}$, as is indicated by the positive mean of Z in all data sets examined, this is probably not enough to explain the large positive values of $\hat{Z}$ for both species in this region. Here the problem is more likely to be a failure of banding data to properly represent the birds killed in the region, mostly because of a lack of banding in the north and preseason movements.

Table 5 indicates a relatively large number of young mallards and black ducks that had moved from the United States to Ontario and Quebec between the summer banding period and the hunting season. For reasons discussed in Chapter 3, this wandering occurs with greater frequency in immatures than adults. It has the effect of increasing age ratios in Canada in a way that cannot be corrected by the banding correction models used in this study, because many of the individuals killed may come from outside the population under study. Without banding that is representative of all populations that come into the study area and are killed, this difficulty can not be further quantified. Such a large part of the Canadian breeding area is not sampled by banding that it is not possible to divide the kill in Ontario and Quebec into

birds from those provinces and birds from elsewhere. Prairie breeding areas may also be sources of dispersing immature birds that inflate the age ratios.

The range of significance of $\hat{Z}$ must be shifted higher for both species. The extent of the shift should be about the same for each, because of the similarity in behavior of the two species. If the approximate range of significance were from -1 to 3 (a shift of 2 units) then the black duck shows a pattern of relative stability, while the mallard shows a decrease in 1972 and increases in 1971, 1973, 1974, and 1980. This agrees with the growth of mallard populations relative to those of black ducks.

Managers want to determine the cause of this relative shift between the two popular sport species. If hunting pressure were to blame, restrictive hunting regulations to protect black ducks would be called for. It may be that other explanations are more important than hunting, however. Two possibilities are direct competition between the species (with mallard benefiting) and environmental changes (changed land use by people, for example) that benefit one species to the detriment of the other. In these latter cases hunting regulations may have little success in preventing the change.

These two categories of cause of change have different effects on the index $\hat{Z}$ used in this study. First consider the effect of excess hunting pressure in a particular year. Hunting occurs after the banding period, so it does not modify $\hat{R}$. $\hat{R}$ critical, however, may be directly affected by hunting, because of the lowered survival rates. Therefore population decreases caused by

hunting (or any other factors) that kill more ducks than are replaced will produce low values of $\hat{Z}$, and should be detected.

On the other hand, suppose that both the birth rate in a region, and the survival rate for birds "born" there remain constant. But suppose that a proportion of the region's young or adults that survive do not return there to breed the next year, but move out of the region. The estimate of R should not be affected, because it relates to the number of young produced in the region per breeding adult. The estimate of $\hat{R}$ should not change either, because it is based on survival rates, and the birds that leave do not die. The estimation of survival based on banding must identify the birds according to the place where they were banded. If they have left that place to summer elsewhere before they are finally killed, we are ignorant of that fact.

This model of regional population change caused by emigration is appropriate both for the case of competition, and for the case of irreversible habitat loss. Neither threat kills individuals, nor need they change production from those birds that stay in the region to breed. They are therefore not reflected in survival rates or $\hat{R}$, and may not be reflected in $\hat{R}$ or $\hat{Z}$.

Toft et al. (1982) suggested that a major mechanism of competition among dabbling ducks is through early nest initiation. Mallards and black ducks interbreed freely and have little or no interspecific behavior such as displays that clearly are not intraspecific behavior between apparent conspecifics. The means of competition, if it exists, must then be based on the same sort of factors that are density-limiting for the individual

species. The logical conclusion is that competition would involve territorial behavior at nesting or feeding areas (Dzubin 1969). Toft et al. (ibid.) found that the mallard was a very early nest-initiator, thereby occupying breeding habitat to the exclusion of other species. Laperle (1974) found, at Lake St. Louis, Quebec, that Mallards initiated nests 2 days earlier than black ducks, on average. This might be sufficient in areas where competition for nest sites is severe to give mallards an advantage. Coulter and Miller (1968) working at Lake Champlain, found that mallards initiated nests about a week later than black ducks. At this point it is appropriate to consider Batt's (1979) suggestion that nest initiation date is genetically determined in mallards (and presumably other ducks). It could be that earlier nesting may be a key to the increasing success of mallards in Ontario. If so, then this would indicate a genetic change in eastern mallards. Do Lake Champlain mallards still initiate nests later than black ducks?

Another possibility, that habitat change is making some areas unsuitable for black ducks, but leaving them acceptable for mallards might also have no effect on the indices obtained in this study. Again, this will happen if the change does not cause decreased survival of birds that had been banded in the region, but removes the birds from the region before the start of the hunting season.

In the same way the apparent stability in prairie mallard numbers from 1975 to 1980, despite indices of surplus production in that period, may be explained by removal of breeding habitat in a way that does not decrease survival of immatures or adults. During dry periods in the prairies (of which 1975-80 was one) low

water levels in the summer allow farmers to cultivate or drain wetlands so that they will not hold water the next spring. Birds from that area that return the next spring will find fewer favourable nesting areas and so may move to breed out of the region, or forego breeding altogether and make a moult migration out of the region. (Smith, 1970, Hansen and McKnight, 1964).

A more detailed study that took into account movement among regions would be required to answer these questions.

Figure 64 shows estimates of age ratio for both mallard and black duck in Ontario and Québec under the same model (C4A). These are roughly similar, suggesting that production in both species responds to the same environmental factors. The mallard generally enjoys a higher production index than the black duck. The relative success of the mallard may be explained in part by a higher production of young (which is shown by this study) and in part by the displacement of breeding black ducks (which is measured by these methods only in so far as it affects the average production from black duck pairs that breed in the region.) The values of Z in Table 37 provide no evidence that hunting is responsible for declines in black ducks in Ontario and Quebec.

4. Blue-winged Teal. Blue-winged teal in Ontario and Quebec show a relative bias in the measurement of R and $R_{critical}$, as is apparent in most data sets. In this analysis combined data were used to estimate an age ratio over the study period, which is compared to values of $\hat{R}_{critical}$ from all of Canada during the study period. Every estimate of $R_{critical}$ is less than the long-term estimate of R . The mean value of $\hat{R}_{critical}$ is .84, compared to the adjusted ratio from wings, 1.91.

FIGURE 6† COMPARISON OF AGE RATIOS FOR MALLARD (---) AND BLACK DUCK (—) IN ONTARIO AND QUEBEC.

In the prairies the analysis and results are similar. The values of $\hat{Z}$ are less because of the reduced precision of estimation from the wing sample.

Blue-winged teal are among the first migrants, with adults leaving early during the hunting season and following different routes from the young, a higher proportion of which head east before moving south. This can cause a change in adult:young proportion in both the source and destination regions between the time that the populations are sampled by banding and the time the birds are killed. Again, with better samples of band recoveries it would be possible to make models such as those in this study, with finer divisions of time and distance to allow for better estimation in this species.

5. Wood duck in Ontario and Quebec. The results for wood duck show little relative bias in the two measurements of $\hat{R}$. A direct interpretation of the results indicates a shortfall in recruitment in 1972 and 1977, and surplus recruitment in 1971, 1976, and 1979. These years of higher age ratios are however those with less precise measurements of adjusted age ratio, primarily because of unusually small adult band recovery. Many of the wood duck killed are from production out of the region, mostly in the United States. (See Table 5.) It may be that in some years weather conditions are suitable for extraordinary immigration of young wood duck from the south before the hunting season. If this is the case, the assumptions of the methods used in this study would apply less closely in those years.

Heusmann (1984) considered the effect of weather on wood duck production from 1979 to 1982 in Massachusetts. During that period the highest production of young was in 1979. Heusmann found that cold and excessively wet conditions during the breeding season both contributed to lowered production of young. The poor breeding conditions in 1972 have been mentioned for other eastern data sets.

6. Other comparisons of $\hat{R}$ and $\hat{R}_{critical}$. With the foregoing discussion of a relative bias between $\hat{R}$ and $\hat{R}_{critical}$ the pintail and green-winged teal have results that are consistent with each other. Despite the lack of high precision, due primarily to low samples of adult band recoveries, good agreement was found for both these species with the July production surveys. (See the previous section). Low production of pintails relative to survival are indicated in 1971, 1974, 1977, and 1980, while surplus production is indicated in 1973, 1975, and 1976. The poor green-winged teal banding samples prevent

a detailed interpretation of results.

Results for gadwall showed consistency between the two estimates of R , though it was not possible to produce annual results. In the case of the American wigeon, poor banding samples caused rejection of all the "A" and "AS" models so there was no correction for relative vulnerability. The production indices thus obtained are suspect because of the known heterogeneity of V among years.

Among the analyses performed 6 data sets provided values of $\hat{Z}$ that allowed examination of the results with acceptable levels of precision. In some other cases the adjusted age ratios are still the best available indicators of population status that we have, but caution must be used in interpreting results that are not based on "A" or "AS" type models. Whereas $\hat{Z}$ in Table 37 includes an assessment of precision, a more useful index of production would be the ratio $\hat{R} / \hat{R}_{critical}$ when the precision of the index is to be ignored.

We have here the response to Caughley's criticism of the use of age ratios (see introduction.) Age ratios, with survival estimates from banding, can reliably indicate population status. Age ratio information can be collected from hunters on a scale that cannot be matched by other surveys, so that global results, rather than local results, can be obtained. The main limitation in the use of age ratios is that they must be supported by banding samples, which are admittedly poor for many species.

Despite a poor understanding of the best way to analyse weather effects, major weather changes are associated

with changes in the age ratios in several cases. The effect of poor weather in 1972 has been mentioned. For prairie breeding ducks the counts of ponds available for nesting is associated with changes in production. Figure 65 demonstrates the age ratios for prairie mallard together with counts of ponds in southern Saskatchewan. Over much of the period the two have parallel patterns of change, suggesting that the availability of ponds is an important factor in breeding success for mallards. If ponds are limiting during these years, then competition for nest sites should be important then as well. This sort of competition is hypothesized as a likely factor in the concurrent increase in mallards and decrease in black duck in Ontario.

In 1979 an increase in pond numbers was not matched by increased production of mallards. After a prolonged dry period changes in vegetation occur that do not respond immediately when water returns. Nesting cover near dry basins may be killed by drought, for example, especially if the basin is cultivated during the dry period. An increase in the amount of surface water for just one year may not be of direct value to breeding ducks that need protective vegetation for nesting. For this reason, while the number of ponds is a major determinant of prairie mallard production, the number of ponds in the previous year is also important. This helps explain increases in production in 1975 and 1980, following years when pond numbers were high.

Global Population Dynamics of Ducks

In this section two approaches to the study of duck population dynamics are considered. The first deals with the matrix method of Leslie and leads to a consideration

FIGURE 65 AGE RATIO (—) FROM PRAIRIE MALLARD, COMPARED TO
POND INDEX (—·—) FROM SOUTHERN SASKATCHEWAN.

of stable age distributions. The second deals with current research on the effects of hunting on mallard populations. This approach might be enhanced by broadening its data source to include age ratios.

Leslie's model of population change is described by Pielou (1969). A vector

$$\underline{n}_t = (n_{0t} \ n_{1t} \ n_{2t} \ \dots \ n_{kt})'$$

specifies the state of the system. The evolution of the system in time is given by premultiplication by a projection matrix, M:

$$M = \begin{bmatrix} F_0 & F_1 & \dots & F_{k-1} & F_k \\ P_0 & 0 & \dots & 0 & 0 \\ 0 & P_1 & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & P_{k-1} & 0 \end{bmatrix}$$

F_i is the contribution of individuals in category i to n_0 in the next time period. P_i is the proportion of individuals that survive from one category to the next.

Without loss of generality, M has an inverse (this may require that older, sterile categories be dropped from the model, but that is not important for the case of ducks). There is a single real, positive eigenvalue, λ , which specifies a stable age distribution:

$$\underline{n}_{s+1} = A \underline{n}_s = \lambda \underline{n}_s. \quad (32)$$

Under certain conditions on A , for example that any two consecutive F_1 are non-zero (Pollard, 1966), the stable age distribution is of special interest because it is attained in the limit as t increases.

For the duck populations considered here, the age ratio R estimates the F_1 . Individual estimates of F_1 by age category are not available on this global scale. The banding models allow estimation of two survival rates, $S_I = P_0$ and $S_A = P_1$, for $i > 0$. The resulting model has this simple form:

$$M = \begin{pmatrix} R \cdot S_I & R \cdot S_A & \dots & R \cdot S_A & R \cdot S_A \\ S_I & 0 & \dots & 0 & 0 \\ 0 & S_A & \dots & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & S_A & 0 \end{pmatrix}. \quad (33)$$

Following the development in Pielou (1969), the dominant eigenvalue, L , will satisfy:

$$f(L) = L^{k+1} - R S_I (L + S_A L^{k-1} + S_A^2 L^{k-2} + \dots + S_A^k) = 0. \quad (34)$$

This equation was solved in this study by Newton's method using successive approximations:

$$x_{n+1} = x_n - \frac{f(x_n)}{f'(x_n)}. \quad (35)$$

The maximum age was set at 10 years.

Table 38 shows the calculation of L for the black duck in the maritimes. This was the data set for which estimates of age ratio and survival were available for several years, and for which they seemed most stable, to approximate the fixed parameters in equation 33. The calculation of the stable age vector used the formula given by Pielou (1969, formula 3.3, page 38).

The values calculated in Table 38 for L are relatively stable (at least in comparison with those for other data sets). They are also close to 1, which would be expected for populations that are stable in total, as well as stable in composition. L provides another index to population status in a given year, much as does Z (Table 37). The two tables agree that the population parameters indicate decrease in 1972, 1973, and 1977.

The near stability of the maritime black ducks in some years might suggest use of current theory dealing with the harvesting of age-structured populations. Harley and Manson (1981) give a typical development of this theory. When the conditions for the stable age distribution are met, an optimal harvest strategy can be devised by the solution of a linear programming problem. In the case of ducks, this could be used by managers in special situations where regulations could be used to favour the harvest of a certain age group. (This might be accomplished through season dates when age groups migrate at different times). The variation of the parameters over a longer time period, however, show that there is little promise in this approach. Anderson (1975) presents a theory that does not require a stable age distribution.

Table 38 - Stable age distribution of maritime black ducks

Year used for parameters L		Proportions in each age class of resultant Stable age distribution																				
		Imm.	1	2	3	4	5	6	7	8	9	10										
1971	1.36	2357	994	461	214	99	46	21	10	5	2	1										
1972	.69	14	:	9	:	7	:	6	:	4	:	3	:	3	:	2	:	2	:	1	:	1
1973	.74	225	:	121	:	71	:	42	:	25	:	14	:	8	:	5	:	3	:	2	:	1
1974	1.07	650	:	221	:	121	:	66	:	37	:	20	:	11	:	6	:	3	:	2	:	1
1975	1.13	92	:	34	:	23	:	16	:	11	:	7	:	5	:	3	:	2	:	1	:	1
1976	1.21	2212	:	546	:	271	:	135	:	67	:	33	:	16	:	8	:	4	:	2	:	1
1977	.96	345	:	153	:	87	:	50	:	29	:	16	:	9	:	5	:	3	:	2	:	1
1978	1.02	385	:	158	:	90	:	51	:	29	:	17	:	9	:	5	:	3	:	2	:	1
1979	1.56	1960	:	810	:	385	:	183	:	87	:	41	:	20	:	9	:	4	:	2	:	1
1980	1.42	2647	:	1131	:	518	:	237	:	109	:	50	:	22	:	10	:	5	:	2	:	1

For other species, and for black ducks in other areas, this kind of analysis was less promising. The reason was not only that available data were too limited. More often the parameters of the Leslie matrix could be estimated on a yearly basis, but they varied too much among years to allow more than one year's projection of population. In these cases equation 32 does not apply. Table 39 summarizes the results of the calculations made according to this model for several data sets. Rather than showing the resulting age distribution, the ratio of young to adult (compressing the older age classes in the stable distribution) is shown. For comparison, the same results are shown for the black duck in the maritimes.

Table 39 Details of attempts made to forecast stable age distributions using parameters estimated in various years

Species and Place	Year	$\hat{R}$	$\hat{SI}$	$\hat{SA}$	$\hat{L}$
Black Duck Maritimes	1971	1.27	.573	.631	1.36
	1972	.35	.466	.542	.69
	1973	.77	.399	.435	.77
	1974	1.33	.363	.587	1.07
	1975	.89	.418	.764	1.13
	1976	2.04	.298	.599	1.21
	1977	.97	.426	.551	.96
	1978	1.05	.418	.580	1.02
	1979	1.27	.643	.739	1.56
	1980	1.27	.608	.652	1.42
Wood Duck Ontario/Quebec	1971	3.69	.407	.558	2.06
	1972	.94	.231	.475	.69
	1973	1.43	.332	.579	1.05
	1974	1.05	.321	.542	.88
	1975	1.10	.517	.551	1.12
	1976	2.03	.602	.557	1.78
	1977	.31	.307	.430	.51
	1978	1.36	.331	.464	.91
	1979	3.48	.299	.588	1.63
	1980	1.61	.411	.439	1.10

Table 39 Details of attempts made to forecast stable age
 (contd.) distributions using parameters estimated in
various years

Species and Place	Year	$\hat{R}$	$\hat{SI}$	$\hat{SA}$	$\hat{L}$
Mallard	1971	.70	.452	.643	.96
Prairies	1972	.35	.423	.600	.73
	1973	.55	.557	.637	.94
	1974	.76	.470	.730	1.08
	1975	.94	.608	.735	1.31
	1976	.89	.470	.623	1.04
	1977	.85	.534	.715	1.17
	1978	.88	.521	.688	1.14
	1979	.63	.605	.698	1.08
	1980	.73	.484	.553	.90

In Table 39, $\hat{R}$ is the observed age ratio. In a stable situation, none of the parameters would vary among years, and (for stable total population) $\hat{L}$ would be close to 1. A value of $\hat{L}$ that is less than 1 indicates a set of parameters for a model that will decrease in total population not only for one year (as is indicated by a negative value of $\hat{Z}$), but would decrease over a long period of time as the population approached its stable age distribution (while tending to zero).

At present this theory based on stable age distributions can only be used when parameters can be estimated, and when the parameters are fairly constant from one year to the next. On this basis no data set would be acceptable among the data sets in this study. What replaces the stable age distribution for populations that have marked variation in parameters among years, as is the case for the prairie mallard?

Generally, the observed variation in $\hat{R}$ indicates that the age composition of most ducks is not stable. There is still a possibility that the variation is bounded in some way, but varies within these bounds in response to various population influences. The most likely of these factors is the effect of weather. For the purpose of modelling, this must be considered an uncontrolled factor. Useful models must therefore be stochastic. Pollard (1966) describes a stochastic model based on the Leslie matrix method, but it requires fixed probabilities in the projection matrix. A theoretical development allowing for a probabilistic distribution of

the parameters of this model (Cohen, 1979) is of interest, but it seems unlikely that it would be easy to relate this to duck populations in the near future. In effect the unpredictable values for $\hat{R}$ in most data sets mean that the matrix projection methods can not be used.

The study of the effects of hunting on waterfowl populations has changed in recent years. Until the 1970's (e.g. Geis and Taber, 1963) it was felt that the effect of hunting on survival could be shown by a correlation analysis of estimated mortality rate and estimated band recovery rate (from hunters). Anderson and Burnham (1976) showed that this approach is invalid because both estimates are derived from the same banding data sets, and there is enough sampling correlation between them to produce the observed correlations.

It has not proved easy to replace the older methods for studying this problem. Anderson and Burnham posed the question as a choice between hunting acting either as an additive or as a compensatory mortality. (Additive mortality would mean that there is no density-dependent control on mortality, compensatory mortality means that the density-dependent control is so complete that there is no net effect of hunting mortality on total annual survival.) Neither extreme is realistic, but the question posed this way allows instructive hypothesis testing.

In their 1976 paper, Anderson and Burnham rejected the totally additive hypothesis for most of their Mallard data sets, but the analysis was not wholly satisfying, primarily because their model assumed a constant "base" survival (the theoretical survival rate in absence of hunting). One consequence of this is that they could not rule out the possibility that adjustments made to hunting regulations had stabilized survival despite additive hunting effects. They did not reject the hypothesis of total compensation, although this failure does not prove that total compensation exists. The next of model they proposed, while accepting a true non-linear relationship between the level of harvest and

the type of hypothesis most applicable (compensatory, additive, or mixed) is an approximation. They suggested a totally compensatory effect at low harvest rate, and a threshold level of harvest rate above which hunting mortality is largely, or totally additive. The form of this model has not been verified.

This same analysis was repeated by Rogers et al. (1979) again for the Mallard, but with more data. They reached the same conclusions.

In the development of their model of mortality, Anderson and Burnham used a variable, b , to represent the level of compensation. Burnham et al. (1984) used a similar model, with $b = 0$ to represent complete compensation, and $b = 1$ for complete additivity. They sought to estimate b , as an index of the degree of compensation. Again, their model assumed a constant "base" survival rate. The results had considerable lack of precision, with many values of the estimate for b outside the theoretical range (0,1). Taking means of the estimates, the authors concluded that hunting has been largely compensated in males. For females it was unclear whether the data were inadequate (as shown by large confidence intervals for the estimates), or whether there was in fact a large additive component from hunting mortality. They summarized their paper by stating that they felt that hunting mortality was largely compensated, for females as well as for males, and that the misleading results of their study are caused by inadequate data.

It is noteworthy that the most acceptable methods now in use for the study of effects of hunting on populations of North American ducks are based only on banding data,

despite the other information available from kill and population surveys. The reason seems to be the difficulty in combining results with unknown bias from different sources. In this study age ratios were compared with survival rates, with some success, by correction of data for known errors and consideration for sampling error. Kill estimates from United States and Canadian national surveys provide an independent source of information that may someday be included in this sort of analysis, allowing an alternative investigation of the effect of harvest.

From a theoretical point of view it seems that the harvest rate, not the total kill, is required to resolve the question of compensation. It therefore seems that estimates of population must be included, to put total harvest into perspective. However it may be that the compensation/additivity issue is misleading. It is almost certain that b in the above model is neither 0 nor 1, and that some degree of additive effect of kill by hunters is always present.

An index of population change, such as $\hat{R} - \hat{R}^{\text{critical}}$ (that is derived from age ratios and banding) might be found to be functionally related to total kill. If this were the case it would be of direct use to managers. Waterfowl management plans now being made throughout North America deal with kill quotas, not harvest rates. If the quotas were set and measured according to standardized harvest surveys, and their effects measured by methods such as those proposed here, population counts would not be needed. As the analysis of data sets here showed, there is a requirement for more banding data from most species. This might require expensive field work, but it should also be possible to increase band reporting rates by advertising (which is

now almost non-existent) and so achieve the same goal at much less cost.

Comparison of age ratios among species

If age ratios are compared for the species of ducks killed in Canada, diversity is apparent. Does this tell us something about the responses species have made to selection pressure?

Patterson (1979) drew attention to the range of apparent ecological strategies among prairie ducks, in the context of r- and K- selection (MacArthur and Wilson, 1967). He pointed out that waterfowl managers should consider the different characteristics of relatively r- and K- selected ducks, which might respond in different ways to management practices. This is important because most of the analytical approaches to waterfowl management have centred on the mallard, for which most data are available.

The concepts of r- and K- selection correspond to an observed dichotomy among many species of plants and animals. Any species now extant has been successful in propagating itself, and maintaining its hold on the energy and other requirements needed for survival and reproduction. Among the strategies used, we see that some species ensure continuation by great reproductive output. The dandelion may be an example. Others (e.g. man) have put more emphasis on reducing losses of individuals, with lower reproductive rate and longer survival. In the second category we may have species that have adapted mechanisms for coping with crowded conditions. These vague ideas correspond to r-selected

and K-selected species, when those terms are used in an imprecise way.

A more precise consideration of r- and K- selection depends on the population model proposed for the species. The simplest model of population change is the exponential model:

$$\frac{dN}{dt} = rN$$

If this were the correct model of a species' population, selection would have to operate to increase r. (If there were two subpopulations with different values of r, say r_1 and r_2 , then that with the larger value would swamp that with the lesser, so the ratio of the first to the second would grow exponentially with rate $r_1 - r_2$).

Of course, there is a limit to space, and other resources needed by any species so the exponential model can not be correct over the long term for any species.

The first step in generalization of the exponential model is the logistic equation:

$$\frac{dN}{dt} = r \frac{(K - N)}{K}$$

The logistic equation allows that population growth slows as the population nears a stable maximum. If this were the correct model of a species' population, then in so far as r and K are under genetic control, selection may operate on these values. Some adaptations (presumably those that occur when the species numbers

are small) may change r and have little effect on K . These correspond to r -selection. Other adaptations (presumably those that occur when the species is crowded) may have a greater effect on K than r ; these correspond to K -selection. Sometimes an adaptation might change both r and K , then we could compare two adaptations, categorizing one as "relatively r -selected" or "relatively K -selected".

The logistic equation is not adequate to describe the population changes of most species. Among the extensions that seem necessary are age structure, time lag, and other species' interactions.

Age structure can be introduced into the exponential model or the logistic model by the projection matrix methods of Leslie (Pielou, 1969). These are discussed elsewhere in this thesis. Demetrius (1975) showed that if age structure is added to the logistic model, then at least one other parameter, which he called the entropy, H , must be added to show the effect of selection. This means that adaptations that affect r or K in the logistic model are selected conditionally on what the adaptations do to H . However, the theory developed by Demetrius required that the projection matrix values be stationary, i.e., that the requirements for a stable age distribution be met.

A time lag can be introduced into the logistic model by a difference equation. Southwood et al. (1974) investigated a difference equation analogue of the logistic equation:

$$N_{t+1} = (L \cdot N_t^{-b}) N_t$$

where L = the finite rate of increase and b = a measure of density dependence. They found that three parameters were needed to specify this model, but they arrived at an approximation of the r - K -dichotomy.

In their discussion, Southwood et al. went somewhat beyond the results of their modelling. They characterized r -selected species as ones with high birth rates, short generations, sex ratios distorted at birth, efficient mate-finding techniques, and a tendency to overshoot environmental carrying capacity when populations are high. K -strategists had reduced mortality, reduced energy wastage, a disproportionate loss of males, increased body size, stable approach to population equilibrium, and, often, inefficient mate-finding tactics.

Interaction with other species introduces new complications into an effective population model. Models of the Lotka-Volterra type (Pielou, 1969) can be used to accomodate such interactions. If such a model were correct then r - and K - are replaced by complicated functions of species and resource interactions. In this context competition, for example, might modify the effects of adaptations that seem to operate on r or K .

For ducks we know that clutch size is genetically determined, to some extent (suggested by Lack, 1967, Klomp, 1970, more recent evidence from Batt, 1979, and, for geese, Findlay and Cooke, 1983). Clutch size is closely related to R , calculated in this study. How has selection operated on R , or clutch size? Can we categorize groups of ducks on the basis of their ecological strategy?

We know that competitive effects are likely, at some level (Toft et al. 1982). In this study we confirmed that the requirements for a stable age distribution are not met for any of the species that had adequate samples. An analytical approach to the question of r- and K- selection must therefore consider a more detailed population model than has yet been developed.

In figure 66 age ratios from this study are plotted relative to the weight of adult females. This gives a comparison of the species according to two measures of ecological strategy. It would have been useful to show survival rates on this graph, but they can not be estimated for many species. The letters used to identify species are shown in Appendix 8. Because not all species provided enough data for the more detailed models, model R was used for the figure. All years from 1969 to 1983 were combined in the ratio calculation.

Species F is the black duck. From figures 42 and 55 we see that the correction models for this species had a greater relative effect on black ducks than the related mallard, bringing the ratio lower both in the relative vulnerability adjustments, and in the misidentification adjustments. The adjustments of the ratio for the black duck that were shown necessary in this study would bring point F down close to point E, the mallard.

Species T is the bufflehead, for which no identification corrections are now available. The correct age ratio is probably higher than indicated by the uncorrected results.

Species P is the oldsquaw, an arctic nesting species that maintains large population numbers in habitat

Relationship of age ratio to weight of adult females

Figure 86

different from the major breeding areas of the other species considered. It has most clearly evolved a strategy unique among these species.

Species I, the shoveler has extraordinary age ratios that are probably related to movement before the hunting season.

Species A, the wood duck, is especially prone to preseason immigration of adult males from southern breeding areas.

With these observations, figure 66 shows a marked inverse relationship between age ratio and weight. Southwood et al. (1974) characterized K-strategists as having larger body size. Does figure 66 show a gradation from r-strategists (green-winged teal, blue-winged teal) to K-strategists (scoters, mergansers, eiders)?

There is a simpler explanation, one that reduces to an r-selection argument for all species. Lack (1967) commented on the observed relationship in waterfowl between clutch size and the inverse of egg size. He suggested that the clutch size was determined by the amount of food available to the female producing eggs. This idea is supported by Bengston's (1971) finding that ducks can regulate the number of eggs laid according to the food resources available. Lack also explained the lower clutch sizes in oldsquaw and goldeneyes (points P, T, and V in figure 66) by the need for larger food supplies in the eggs in northern breeders. Klomp (1970) concluded that Lack's explanation of clutch size in waterfowl was then the best available.

The pattern in figure 66 then could arrive from the relationship of clutch size and R (R is clutch size, multiplied by the hatching and fledging rates) and the relationship of egg size and the body size (Klopp, 1970 shows that such a direct relationship exists.) This provides no separation of species, except as large, and small. If, as Southwood et al. (1974) suggest, body size is implicated in a dichotomy of evolutionary strategies, this may prove to be a useful categorization.

Suggestions for Improvement in the use of Age Ratios

The most evident shortcoming of this Analysis for many species was the limited banding data that were available. Banding data are needed both for the correction for relative vulnerability, and for the determination of survival estimates.

It may not be realistic to expect great increases in the banding of some species that breed in remote areas. However efforts should be made to increase the reporting of bands by public information.

The sample sizes of wings received were adequate for most species in this analysis. The number of hunters contacted does not have to be increased, but some effort to increase response in remote areas is needed. (A special, later mailing to Newfoundland was tried in 1983, and it doubled the return of sea duck wings.)

A correct analysis of the wing receipts should be done according to the sampling unit, the hunter. Appendix 7 gives some details of the effect of sampling by hunter, instead of by duck. Until 1984 the survey methodology did not allow more than about 70% of the returns to be matched to the hunter. In 1984 a label was included with the survey that identifies the hunter, and will allow a subsequent analysis according to the cluster sampling method.

To date, the development of wing keys has concentrated more on the reliability of the whole determination, rather than on the performance of individual characters. In part this is a result of the scarcity of reliable known age and sex material for many species, but it also reflects the time available for the application of

alternate methods of identification. If a method were used that required several measurements to be taken and entered onto coding forms the time and expense of wing bees might be substantially increased. On the other hand, more objective methods might remove the need for expert identification, and allow some species to be analysed by less specialised staff out of the wing bee context, giving a savings in time and money.

If there were a large sample of wings of incontestable classification, of equivalent freshness to the wing sample (so that measurements will be comparable) it would be possible to develop discriminant functions for the identification of wings of most species. Several discriminant functions would be required, depending on the amount of information available from each wing. This approach would have the advantage of retaining information on the uncertainty in the identification of individual wings. An adult male wing from a particular species may be identified with certainty in some cases, but if crucial features are missing the identification may be dubious. If the survey kept information on characters used in the identification, these two possibilities could each be given the appropriate contribution to the overall uncertainty in the statistics, by considering them in separate subsamples with different discriminant functions. The present emphasis on determination of age and sex as opposed to objective measurement of characteristics does not allow us to distinguish between wings that "key out" on reliable characteristics, and those that are decided on the basis of less desirable rules.

The contention of Boyd (1970) that Canadian mallard wings should be identified first on the basis of distal

characteristics, and only secondarily on the basis of the inner wing, cannot be answered without a complete analysis of the characteristics of Canadian mallard sample wings (and a much better sample of known age material than was available to him). It might turn out that the best discriminating characteristics for Canadian wings with given sets of available feathers are rather more scattered throughout the wing than either Boyd's or Carney's methods suggest.

It is not certain, without an analysis based on individual characters, that the key in use for a particular species makes best use of the characteristics of the wing. For some species the keys now in use have been developed on the basis of a character by character study, but for most the lack of full analysis of known age samples has meant that keys had to be developed by observed separation of unknown wings into categories, with age and sex assigned by analogy with better understood species. Even when characters have been considered individually the published results usually do not show use of recent multivariate analysis methods (such as discriminant function analysis) that could in some cases improve on the keys that are developed.

Variables that could be used in development and enhancement of wing identification keys need not necessarily be continuous. The presence or absence of a particular colour in one area of the wing, or the condition (frayed, unfrayed) of a certain group of feathers are examples of discrete variables that could be used. Measurements of feathers are promising continuous variables that would remove the subjective nature of criteria such as "broad middle coverts". Some measurements might reflect conditions of handling, or

the physiological condition of the bird. Thus broadly representative samples of known age and sex material would be needed.

These comments on the ideal approach to identification of wings are based on observations in this study of the significant shortcomings in the identification methods as now practiced for some species in the Canadian survey. The practical limitations of the survey may, however, allow only for a partial improvement. One problem, already mentioned, is the limited resources available for wing identification. If each wing were to be measured in, say, 5 ways, and if 5 other criteria were to be coded from each wing, the processing time for each wing would be increased substantially, as would the cost of computer data entry and subsequent analysis. On the other hand the objective approach may reduce other costs, such as the need for double checking, and the expenses of travel.

A more serious problem is in the development of reliable discriminant methods themselves. For many species known age material is virtually lacking. The determination of age and sex from hunter killed birds is improved by cloacal, tail, and full plumage examination, but is still subject to error. For many species even this type of known sample is very difficult and expensive to collect. The ideal known age sample, from later recoveries of birds banded as young, is very sparse.

Birds grown under semi-domestic conditions do not seem to be appropriate as standards for development of discrimination techniques. For some species the reason is simply difficulty of culture. In general, however, findings from captive birds are limited by the

fact that feather moult may be very different in the wild than in the captive individual, in part because of modified timing in behavioral patterns, and in part because of changes in physiological condition.

Improvements in identification method will, for the reasons given here, take place gradually. Probably the best approach will be to develop character-oriented identification for some species, while retaining the whole-wing 4 category identification for others.

8 SUMMARY AND CONCLUSIONS

This research started in 1979, with attempts to use the age ratios from Canadian duck wing surveys as indices of production. It was seen that questions of accuracy and precision in the determination of age ratios would be important. Until that time the Canadian survey results were not corrected in any way, nor were estimates made of sampling error. This made it difficult to compare results with other biological data collected from other sources.

In this work corrections, such as are possible, are made for the errors introduced by misidentification, unbalanced sex ratio, and differential vulnerability of the age and sex classes. Estimates of sampling error are produced.

One important question is, when is it possible to ignore the effects of error sources, and treat the results as "trend" indices, if not accurate measures of "level"? The answer to this varies not only by species, but also by region. It was found, generally, that corrections for relative vulnerability should be applied on a yearly basis. The effect of this differential vulnerability is heterogeneous among years. The extent of this heterogeneity is sufficient to produce large differences in the uncorrected age ratio, even when no change in production has taken place.

For some species, such as the black duck, the errors made in identification must be controlled. Otherwise they introduce significant error. There are many species for which identification could be a problem, but for which adequate information is lacking. Generally,

failure to control for misidentification causes overestimation of the age ratio, but this is not a simple relationship.

A method is developed to relate the age ratio to the survival of adults and immatures, as determined from band recoveries. This can be used to monitor the change in a population that is not subject to emigration or immigration. If hunting were a major cause in the observed decline of black ducks in Ontario and Quebec, this method should have given an indication. It did not. A conclusion is that the decline in black ducks is related to factors other than hunting, such as change in habitat, or competition with mallards, although the effects of hunting can not be ruled out altogether.

The index of population change should have a zero mean, but has a positive mean in most cases. This implies either that there is a positive bias in survival estimates from banding, or a positive bias in the estimation of R . The first sort of bias could result from heterogeneity among birds banded (Pollock and Ravelling, 1982), the second from the cluster-based sample used in the wing survey. Both effects are probably present to some extent.

Several species were considered under the assumptions needed for the theory of stable age distributions. It was generally found that the parameters of birth and survival vary too much from year to year for duck species for this theory to be applicable.

One reason why it was important in this study to remove biases and attempt to measure "level" rather than trend, was to allow the combined analysis with other data sources. The use of survival estimates from band recoveries was the most important such combination. The

change-in-ratio method (Seber, 1982) was used to combine duck wing survey data with estimates of kill by hunters, from a mail survey. This attempt produced an estimate of population similar to what is known from aerial surveys, but the approach makes unrealistic assumptions.

Throughout the analysis a main observation was the heterogeneity of data. This was manifested in variable recovery rates from banding, variable relative vulnerability, and unusual behavior of the correction models for some data sets. A method was developed to allow correction for relative vulnerability of age, sex, or other categories. Smaller analysis regions may have been desirable, but would not have produced good samples.

It is not certain that the birds sampled for banding are the same as the birds sampled several weeks later in the same places by hunters. This question of "source of birds" might be addressed by expanding the analysis regions to encompass the entire area where the population of interest occurs, but this invites difficulties in heterogeneity as mentioned above, and in the fact that the age ratios are not static but change through the hunting season.

It is intriguing to think that the variation in age ratio that is observed among North American ducks is related to different evolutionary strategies. This may be so, but there is no reason from theory now available to reject Lack's hypothesis that clutch size (which is correlated with age ratio) is determined by the food available to the female, thus to the inverse of egg size, and thus to the weight of the bird.

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Appendix IThe choice of models in production of survival estimates

Of the models included in program BROWNIE, 3 were used in the results shown in Table 2. The assumptions of these models are:

H02 - Young and adults have different survival and recovery rates. Survival rates do not vary. Recovery rates are year-specific.

H1 - Young and adults have different survival and recovery rates, both of which vary year to year.

H2 - An extension of model H1 allowing different recovery rates for newly banded birds as opposed to those banded previously. (This changes the first year recovery rates for adults.)

Banding data were selected for all species and regions included in this report. Only those data sets in Table 2 had the minimum samples needed for analysis.

Models were chosen as follows:

Wood duck, Ontario and Quebec

Two models fit adequately well, so two sets of results are presented. Model H1 gave the best fit (probability of a more extreme chi-square was .172). Model H02 had a corresponding index of fit of $p = .04$.

Green-winged teal

Only model H1 was acceptable ($p = .139$).

Gadwall

The best model was H1 ($p = .083$), but some estimates were unrealistic, so the average of values for all years is used in Table 2. The covariance of (S_A, S_I) was averaged, as well, with the assumption of independence among years.

Black duck in the maritimes

The best model was H1 ($p = .069$).

Black duck in Ontario and Quebec

No models gave a good fit. The mean results from model H2 were used ($p = .003$).

Pintail

The best model was H1 ($p = .066$).

Mallard in Quebec and Ontario

No model gave a good fit. The mean results from model H2 were used ($p = .000$).

Mallard in the prairies

The best model was H1 ($p = .073$).

Blue-winged teal

The best model was H1 ($p = .326$).

Redhead

The best model was H02 ($p = .444$).

Lesser scaup

The best model was H02 ($p = .476$), although run-time errors (division by zero) occurred during analysis of the data, making the results suspect.

American wigeon

The best model was H02 ($p = .137$).

Common eider

There were not enough young banded to use the program BROWNIE. Instead the program ESTIMATE, which provides estimates from adult bandings only, was used. The best model was 1, although the fit was poor ($p = .000$). No estimate of covariance of S_A and S_I was available. R is calculated from equation 8a.

Appendix II

Identification methods for particular species

In this description of methods for wing identification "Carney" refers to Carney (1964), the primary source that has been used at Canadian (and U.S.) wing bees. Carney has also distributed a useful tabular summary of the wing identification methods that gives some additional information. "Boyd" refers to Boyd Harrison and Allison (1975), the primary source for the British wing survey. Other sources are given full citations.

The discussion of identification clues is kept brief as possible, yet still retains the essential information. The structure of identification keys is implied in the order of presentation. Characteristics thought to be "diagnostic" (fully reliable) are indicated. (Although there are degrees of confidence even in "diagnostic" criteria. Hormonal variations in birds occur regularly and may obscure even the most straightforward identifications. Most of the "diagnostic" criteria have some degree of error, a level of 5% is generally considered acceptable. Boyd only claimed that one criterion was "diagnostic" without supportive evidence in the European birds he studied, (that is the white shoulder of the AM European wigeon).

Some general comments apply to most species. Fraying and fading are signs of immature tertials, tertial coverts, and greater tertial coverts in many species, although this clue is of reduced significance in diving ducks and does not apply at all in the case of adults that have not moulted by the start of the hunting season (a state

that is rarely but consistently encountered in females of some species, presumably those with very late broods). Also, late season adults, or adults from areas with very early moulting dates may show signs of wear.

Tertials are often distinctive but those usually acquired in the fall by young birds are similar to those of later plumages. A Juvenile tertial therefore is diagnostic but adult type tertials are not.

Greater, middle, and lesser coverts of immatures are often small, narrow, tapering and rough in appearance compared to those of adults. Primary coverts of immatures tend to be narrow and have a more tapered tip than adults. Adult wings tend to be larger than immature wings and male larger than female, although there is often considerable overlap in sizes among the four categories.

Carney had to develop his keys with limited known age / sex material for some species. He gives the number of known wings he had available for two of the less frequent species:

Species	Known wings available to Carney
Bufflehead	25
Hooded Merganser	0

The criteria given by Carney are, for the most part, those used at wing bees. However many wing bee participants have particular knowledge of wings of some species that is used as well. This comes primarily from field experience in banding, bag checks and hunting. Unfortunately this sort of knowledge is not documented.

Mallard

Carney - diagnostic characteristics of sex
 Vermiculated scapulars - M. Vermiculated
 proximal under-wing coverts - M. White bar
 anterior to speculum extends over tertails - F.

Carney - age determination For Males age criteria
 are taken in sequence from greater tertial
 coverts (most important) tertials, primary
 coverts (light edging) and middle coverts. For
 females age criteria are taken in sequence from
 greater tertial coverts (including lack of
 white edging on two most posterior feathers),
 tertials, primary coverts (in females light
 edging must be conspicuous to imply immaturity)
 and middle coverts.

Boyd - additional criteria from European wings may
 be of use with North American mallards. Boyd
 uses the colour of under tertial coverts to
 indicate sex (barred or spotted sepia in F),
 the colour of lesser and middle coverts as a
 clue to age in males (brown, IM, grey-brown,
 AM), and shape of the tips of the 4th 5th and
 6th greater coverts as another (small and
 rounded in I, large and angular in A). Well
 defined cream or buff margins are found in AF.

Gatti (1983) reported on some discriminant
 function analysis for the identification of
 mallard wings. He took the approach of using
 either all quantitative or all qualitative
 characteristics. He found that the most useful
 of the qualitative characteristics tested for

identification to age were white edging on the primary coverts and the shape of the middle secondary coverts. He also developed two discriminant functions based on quantitative measurements, where the width of the greater secondary covert 5 performed well alone, and better in conjunction with 4 - 8 other measurements. One limitation of the analysis for the purposes of the wing surveys is that the known age sample was identified according to the methods of Carney. Since the two qualitative characteristics mentioned are also used in Carney's key it is perhaps not surprising that they performed well as discriminants.

Gatti also reported significant difference in feather measurements between penned and wild mallards.

Krapu Johnson and Dane (1979) described a discriminant function analysis of wing feather criteria for identification of age in wild mallards. All known age birds were taken from the wild and penned throughout the study. Size measurements and 1 colour measurement were taken from 3 primaries, 1 primary covert, the alula, and 5 greater secondary coverts. The most useful single measurement they found was the black-white surface area of greater secondary covert 2.

Henny and Ludke (1974) attempted to develop an aging technique for mallards based on the weight of eye lens protein, but found too

little change in mallards over 8 - 9 months old to allow a useful method.

Black duck

Carney, in his original key, gave a method that did not involve measurement of the wing as a characteristic for sex determination of immature birds. A revised method that was thought to be better for the Canadian wing sample has been in use in Canada since c. 1971. The method, an adaptation of Carney's, involves a first determination of age, from tertials, greater tertial coverts, primary coverts, and middle coverts. Wings that can be measured are assigned to a sex according to length (adults, $F < 280$ mm., immatures, $F < 272$ mm., M otherwise). Other wings are assigned to a sex on the basis of colour pattern in the speculum. Adult wings with primaries not fully grown by September are female (diagnostic).

Gadwall

Carney characterises AM by the colouring of middle coverts. Tertials, greater tertial coverts, and posthumeral characterise immatures. Middle coverts have distinctive patterns that separate IM from IF and a measurement is also given ($IF < 259$ mm., $IM > 260$ mm.)

Boyd points out the difficulty of distinguishing IM Gadwall from AF in the British sample.

Oring (1968) described the plumages of the Gadwall. Of particular interest is the sequence and timing of moults that are taking place

during the hunting season. At this time adults of both sexes are moulting into Alt. Plumages. Adult males dropped their Basic tertials between 10 November and 14 December (or later), while females retained their Basic tertials until January to March. Immature females retained their tertials until February to June, while immature males moulted tertials from November to February. Some birds retained the juvenal scapulars. Orings study was based primarily on penned birds.

American wigeon

Carney - all middle coverts white - AM (diagnostic).

Carney - evidence of IM - Vermiculated scapulars (diagnostic), colour of middle coverts, colour of greater coverts in wings thought to be immature based on tertials and tertial coverts.

Carney - separation of IP and AF - tertials and tertial coverts, colour of middle and greater coverts.

Boyd gives details on the European Wigeon that might provide new characters of use.

Wishart (1981) describes a study to determine criteria for the age separation of American Wigeon based on wing feathers. This was a discriminant function analysis based on known birds from a penned flock, and on a sample of wings taken from the Western Canadian wing bee and classified according to the criteria

established by Carney. colour patterns in the greater secondary coverts and the middle secondary coverts, and measurements of the greater secondary coverts and primaries were evaluated. He found that males could be aged by the colour of the middle secondary coverts. Females could be aged by the colour pattern of 3 feathers, the middle secondary coverts, greater secondary covert 5, and greater secondary covert 3, for an accuracy of 93% in females, and 100% in males. He found differences between wild birds and penned birds in feather measurements.

Green-winged teal

Carney - sex determination - the tertial has a longitudinal dark stripe. In F this tends to be brownish and grades into the basic feather colour. In M the stripe is black and sharp-edged. In M vermiculated scapulars are diagnostic. M tend to show more buffy edging on tertials than F. A measurement is used ($M > 179$, $F < 160$).

Carney - age determination from tertials, greater tertial coverts, primaries (in M), primary coverts, middle coverts.

Boyd gives criteria for identification of the teal. Although this is the same species as occurs in North America there are several important differences in the plumages of the two subspecies. Some characteristics used by British workers that may be of use here include the amount of green in the secondaries and colour in the greater coverts as clues to sex.

Blue-winged teal

Carney - sex determination - no iridescence in the speculum characterises F. Visible portion of greater secondary coverts white in M.

Carney - age determination in M - greater tertial coverts, greater secondary coverts, tertials.

Carney - age determination in F - tertials, greater secondary coverts, greater tertial coverts.

Shoveler

Carney - sex determination - iridescence of speculum and colour of middle coverts and lesser coverts.

Carney - age determination in M - tertials, middle and lesser coverts, greater tertial coverts, greater coverts.

Carney - age determination in F - tertials, greater tertial coverts, greater secondary coverts.

Boyd states that pale blue lanceolated scapulars indicate M.

Pintail

Carney - sex determination - vermiculated scapulars M (diagnostic), black longitudinal stripe on tertials M (diagnostic), iridescence of speculum and colour of most distal secondary.

Carney - age determination in M - tertial coverts, tertials, middle coverts.

Carney - age determination in F - tertials, tertial coverts, greater coverts, middle coverts (distinctive pattern).

Boyd mentions a sex-based difference in under wing coverts in British pintail (peppered or vermiculated in M, light brown with margins or barring in F). The greater tertial coverts and posthumeral are used in aging.

Wood duck

Carney - sex determination - one or more pink greater tertial coverts F, shape of white trailing edge on secondaries (tear-drop F, even width M).

Carney - age determination in M - tertials, scapulars, colour of greater and middle coverts, shape of most proximal greater covert.

Carney - age determination in F - tertials, greater tertial coverts, colour of greater and middle coverts, shape of most proximal greater covert.

Redhead

Carney - sex determination - vermiculated tertials or scapulars M, some IM separated from IF by flecking on lesser or middle coverts.

Carney - age in M - greater coverts.

Carney - separation of AF from immatures -
tertials, greater coverts.

Boyd gives details of identification of pochards that may be of limited use for the redhead. In particular the identification of immature pochards is determined by the colour and extent of flecking or vermiculation in several feather groups. A measurement is also used to aid determination of age in pochards.

Dane and Johnson (1975) describe an investigation of identification techniques for female redheads. Their known sample was determined using the criteria of Carney, so their findings are subject to the accuracy of this technique. They wanted to find characteristics among feathers that would not moult until after the following breeding season. They included patterns on and width of the greater secondary coverts, and size of primary feathers. Their best variables for the separation into age classes were greater secondary coverts width, greater secondary coverts pattern, and the weight of the 5th primary.

Canvasback

Carney - AM is distinctive. So are IM in stages of moult into AM type tertials or greater tertial coverts. IF have little or no flecking on middle and lesser coverts, IM have well flecked greater coverts, often forming tipping over secondaries, AF also have well flecked greater coverts, but concentrated near ends of coverts, no tipping, and the shape and texture of adult feathers.

Greater scaup

Carney - sex determination - amount of white in scapulars (M > 50%), flecked or vermiculated tertials (M), large flecks on middle coverts recessed from feather edge (M).

Carney - age determination - tertials, greater coverts, middle coverts.

Boyd gives a measurement for identification of sex (M > 220 mm., F < 220 mm.)

Billard and Humphrey (1972) describe moults and plumages in the greater scaup. They found that the time of most intensive moult (during or near the hunting season) in the scapulo humeral region was in October to December (AM), November to December (IM) October to November (AF) and December (IF). Most birds were collected in Connecticut.

Lesser scaup

Carney - as for greater scaup, with caution that the characters may look somewhat different.

Ring-necked duck

Carney - determination of age - tertials, greater coverts, middle coverts.

Carney - sex determination in A (not given for I) - tertials, middle and lesser coverts, edging on gray secondaries, flecking on lesser coverts.

Common goldeneyeBarrow's goldeneye

(Carney did not give complete information for the separation of these two species in his key. Carney (1983) describes a technique for this separation and for further identification that will supplant the older method. P. Dupuis (pers. comm.) has developed another key for Goldeneyes that is based in part on patterns in the middle coverts. Dupuis' new key was consistent with Carney's new method for Goldeneyes examined during 1983 wing bees in Canada, and for some wings was easier to apply. A combination of the methods should probably be used.)

Carney (up to 1983) - AM is distinctive. AF supported by tertials, colour and shape of greater coverts. If present, scapulars decide sex of I. Without scapulars, I are sexed by measurement ($IF < 210$, $IM > 215$).

Boyd gives a measurement for separation of the sexes that is somewhat smaller at the dividing point (this probably relates more to differences in British and American goldeneye than to differences in measurement method, the American race being larger). The measurements would be consistent for most wings (Boyd gives $M > 210$ mm., $F < 207$ mm.)

Carney (1983) gave an updated key to goldeneye wings. The AM is distinctive. Banding on the greater secondary coverts and colour patterns in the middle secondary coverts and lesser secondary coverts identify AF. The immatures

are sexed by measurement ($IM \geq 218$ and $IF < 218$ in Barrow goldeneye, $IM \geq 213$ and $IF < 213$ in common goldeneye).

Bufflehead

Carney - AM distinctive. IM are next determined by measurement ($IM > 159$, AF, IF otherwise). Age of immatures determined by greater coverts and tertials.

Ruddy duck

Carney - age determined by tertials, greater tertial coverts, and middle coverts. No method is given to separate sexes.

Common merganser

Carney - AM distinctive. AF distinguished from I by tertials, greater tertial coverts, and black terminal bar on greater secondary coverts. Sex of I determined by measurement ($IM > 258$, $IF < 258$).

Boyd gives a measurement for the separation by sex of all ages of the goosander that differs somewhat from the North American measurement ($M \geq 280$, $F \leq 270$).

Red-breasted merganser

Carney - AM distinctive. AF distinguished from I by tertials, greater secondary coverts, greater tertial coverts. No method to identify sex of I is given.

Boyd gives a measurement for the separation by sex of all ages ($M \geq 244$, $F \leq 230$).

Hooded merganser

Carney - determination of age - AM mostly pale grey middle coverts. IF separated from I by middle coverts, tertials, and greater coverts. Sex of I cannot be determined unless some AM middle coverts show on moulting IM.

Oldsquaw

Carney - AM are identified by the colour of the wing. AF separated from I by middle coverts, tertials, and greater coverts. I are not separable by sex.

Boyd gives a detailed identification that separates the summer and eclipse plumages of the adult, and identifies the immatures as to sex. A measurement is given for sex ($M \geq 219$, $F \leq 210$). Boyd emphasizes the importance of the scapulars for oldsquaw identification.

Peterson and Ellarson (1978) related the colour of female oldsquaw scapulars to breeding condition as evidenced by the Bursa of Fabricius, the ovaries and the oviducts. They concluded that oldsquaw do not breed until at least 2 years old, as had been thought, and that female oldsquaws past the year of birth show a continuum of colour in the scapulars, from grey in the non-breeding subadult to brown in the female several years older.

Common eider

Carney - AM are distinctive. AF identified by rufous edging on tertials, white tipping on

secondaries, greater tertial coverts, and rufus edging of middle coverts.

The common eider does not breed until at least 3 years of age (Mendall, 1968, quoted in Bellrose, 1978, but see Baillie and Milne, below). It is clear that Carney's criteria are for adults (probably of breeding age) as one group, and juveniles and subadults grouped as immatures. A. J. Erskine, P. Dupuis, and I have attempted to divide the common eiders at wing bees in 1981 and 1983 into adult, subadult, and immature classes. Known age material would allow verification of the method used.

Boyd gives a detailed method for identification of common eiders. He divides into several age classes using criteria similar to those proposed for the Canadian wing bees. In males he has 4 age classes, and in females 3. This corresponds to the groupings of wings that were apparent in the Canadian sample.

Baillie and Milne (1982) found that some female common eiders in Scotland do in fact breed at two years old, but with low success. The hormonal effect of this on plumage may be important, in view of the relationship between breeding condition and scapular colour in Oldsquaw.

Black scoter

Carney - wing shiny black in AM, and 10th primary is attenuated. AF and I distinguished by tertials, greater tertial coverts, and middle coverts.

Boyd gives a measurement to divide the sexes ($M \geq 228$, $F \leq 229$).

White-winged scoter

Carney - shiny black middle and lesser coverts distinguish AM. AF separated from I by tertials, tertial coverts, scapulars (if present), and greater coverts. No method is given for sexing I.

Boyd gives a measurement to identify sex of immatures ($M \geq 269$, $F \leq 251$). He suggests that minimal dusky tips on the greater secondary coverts may indicate subadults.

Surf scoter

Carney - AM are identified by shiny black wing colour with adult tertials and greater tertial coverts. AF and I are separated by middle coverts, greater tertial coverts, and tertials.

Additional measurements from U.S. samples

In his tabular summary of wing bee identification methods Carney provided additional measurement criteria:

Species	Measurements given in mm.			
	AM	IM	IF	AF
Black Duck	81% ≥ 252	90% ≥ 248	90% < 248	81% < 252
Gadwall	88% > 262	88% ≥ 258	88% < 258	65% < 258
A. Wigeon	91% ≥ 255	86% ≥ 250	86% < 250	91% < 255
N. Shoveler	88% ≥ 236	86% ≥ 229	88% < 229	93% < 236
N. Pintail	88% ≥ 264	97% ≥ 258	94% ≤ 258	86% < 264
Wood Duck	69% ≥ 222	70% < 222	68% < 215	66% ≥ 215
Canvasback	88% ≥ 232	85% ≥ 227	84% < 227	88% < 232
G. Scaup	75% ≥ 218	83% ≥ 216	87% < 216	75% < 218
L. Scaup	74% ≥ 200	77% ≥ 198	67% < 198	82% < 200
R.-necked Duck	82% ≥ 192	82% ≥ 189	86% < 189	93% < 192
C. Goldeneye	94% ≥ 218	97% ≥ 210	98% < 210	98% < 218
B.'s Goldeneye	97% ≥ 222			96% < 222
Bufflehead	93% ≥ 162	98% ≥ 158	97% < 158	99% < 162
C. Merganser	99% ≥ 258	99% ≥ 250	97% < 250	99% < 258
R.-b. Merganser	94% ≥ 230	89% ≥ 222	99% < 222	97% < 230
H. Merganser	82% ≥ 191	79% ≥ 184	76% < 184	77% < 191
C. Eider	66% ≥ 285	71% ≥ 271	72% < 271	71% < 285
Black Scoter	81% ≥ 224	83% ≥ 218	81% < 218	86% < 224
W.-w. Scoter	90% ≥ 275	87% ≥ 267	85% < 267	93% < 275
Surf Scoter	81% ≥ 233	68% ≥ 229	70% < 229	88% < 233

Others methods of aging and sexing ducks have been proposed. Woodall (1981) tried to establish criteria for identification of the Redbilled Teal. Because of the rapid achievement of adult size in this species Woodall found no age related differences in 11 measures of size.

There were sex related differences in almost all characteristics examined. Younger juveniles could be aged by belly plumage, and later in the year the best aging criterion was the microscopic appearance of the tunica albuginea. Sex could be determined by the presence of a penis, size, and a few plumage characteristics.

Appendix III Identification matrices obtained during this study

SPECIES: BLUE-WINGED TEAL

YEAR: 1978, 1979, 1981

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	MI	IF
AM	10		3	1
AF		12		3
MI	3		48	
IF		2	1	36
	AM	AF	MI	IF

RESULTING IDENTIFICATIONS

SPECIES: WOOD DUCK

YEAR: 1978 TO 1982

TYPE OF SAMPLE: BANDING

KNOWN	AM	AF	MI	IF
AM	1		1	
AF		3		
MI		1	10	
IF	1	3		5
	AM	AF	MI	IF

RESULTING IDENTIFICATIONS

SPECIES: BLUE-WINGED TEAL

YEAR: 1978 TO 1982

TYPE OF SAMPLE: BANDING

KNOWN	AM	AF	MI	IF
AM				1
AF		5	2	
MI	1	1	14	3
IF			1	13
	AM	AF	MI	IF

RESULTING IDENTIFICATIONS

SPECIES: COMMON EIDER

YEAR: 1978-1982

TYPE OF SAMPLE: BANDING

KNOWN	AM	AF	MI	IF
AM		4		1

SPECIES: WOOD DUCK

YEAR: 1978, 1979, 1980, 1981

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	MI	IF
AM	41		5	
AF		20		2
MI	2		26	
IF		3	1	26
	AM	AF	MI	IF

RESULTING IDENTIFICATIONS

SPECIES: MALLARD

YEAR: 1978

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	MI	IF
AM	4		2	
AF		7		3
MI	1		16	
IF			2	16
	AM	AF	MI	IF

RESULTING IDENTIFICATIONS

Appendix III Identification matrices obtained during this
(contd.) study

SPECIES: PINTAIL

YEAR: KNOWN SAMPLE 1978, 1979 AND BANDING 1978 TO 1979

TYPE OF SAMPLE: KNOWN CONTROL AND BANDING

(1 AM CALLED NM, AF CALLED IF
WERE ERRORS FROM BANDING COMPARISON)

KNOWN	AM	AF	NM	IF
AM	5		2	
KNOWN		11		1
AF			1	
KNOWN			10	15
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

SPECIES: AMERICAN WIGEON

YEAR 1978, 1979, PLUS BANDINGS

TYPE OF SAMPLE: KNOWN CONTROL AND BANDINGS

(NO ERRORS FROM BANDING COMPARISON)

KNOWN	AM	AF	NM	IF
AM	9			
KNOWN		4		
AF		1	10	
KNOWN		1		16
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

SPECIES: HOODED Merganser

YEAR 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	NM	IF
AM	4			
KNOWN		3		
AF				1
KNOWN			1	2
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

SPECIES: GREEN-WINGED TEAL

YEAR 1978, 1979, 1980, 1981

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	NM	IF
AM	41		7	
KNOWN	2	23	2	6
AF	6		55	4
KNOWN		1	3	42
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

SPECIES: LESSER SCAUP

YEAR 1978, 1979, 1981

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	NM	IF
AM	8		2	
KNOWN		4		
AF		2	12	
KNOWN			1	14
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

SPECIES: GREEN-WINGED TEAL

YEAR 1972 TO 1982

TYPE OF SAMPLE: BANDING

KNOWN	AM	AF	NM	IF
AM	1	1		
KNOWN		4	2	3
AF	1	1	6	1
KNOWN			2	6
NM				
KNOWN				
IF				
	AM	AF	NM	IF

RESULTING IDENTIFICATIONS

Appendix III Identification matrices obtained during this
(contd.) study

SPECIES: REDHEAD

YEAR: 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN AM	5			
KNOWN AF	1	1		
KNOWN IM			10	
KNOWN IF			2	14

AM AF IM IF
RESULTING IDENTIFICATIONS

SPECIES: GADWALL

YEAR: 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN AM	4			
KNOWN AF			1	1
KNOWN IM			12	2
KNOWN IF				8

AM AF IM IF
RESULTING IDENTIFICATIONS

SPECIES: GREATER SCAUP

YEAR: 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN AM	2			
KNOWN AF		1		1
KNOWN IM		1	6	4
KNOWN IF			1	1

AM AF IM IF
RESULTING IDENTIFICATIONS

SPECIES: BUFFLEHEAD

YEAR: 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN AM	2			
KNOWN AF			1	1
KNOWN IM			1	
KNOWN IF		1	1	4

AM AF IM IF
RESULTING IDENTIFICATIONS

SPECIES: CANVASBACK

YEAR: 1978, 1979

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN AM	2			
KNOWN AF		1		2
KNOWN IM			11	
KNOWN IF				13

AM AF IM IF
RESULTING IDENTIFICATIONS

SPECIES: RING-NECKED DUCK

YEAR: KNOWN SAMPLE, 1978, 1979 AND BANDING 1978 TO 1982

TYPE OF SAMPLE: KNOWN CONTROL AND BANDING
(2 ERRORS FROM BANDING COMPARISON)

KNOWN AM	1			
KNOWN AF		1		1
KNOWN IM	1		3	2
KNOWN IF				8

AM AF IM IF
RESULTING IDENTIFICATIONS

Appendix III Identification matrices obtained during this
(contd.) study

SPECIES: MALLARD

YEAR: 1979

TYPE OF SAMPLE: KNOWN CONTROL FROM EASTERN WING BEE

KNOWN	AM	AF	IM	IF
AM	10		3	
AF		3	1	2
IM			18	1
IF		1		10
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

SPECIES: MALLARD

YEAR: 1980

TYPE OF SAMPLE: KNOWN CONTROL-EASTERN WING BEE

KNOWN	AM	AF	IM	IF
AM	10		5	
AF		18		6
IM	1		23	1
IF		1		22
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

SPECIES: MALLARD

YEAR: 1979

TYPE OF SAMPLE: KNOWN CONTROL FROM WESTERN WING BEE
(EXCLUDED FROM ANALYSIS)

KNOWN	AM	AF	IM	IF
AM	18		3	1
AF	1	5	1	10
IM			15	1
IF		4	1	12
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

SPECIES: MALLARD

YEAR: 1978 TO 1982

TYPE OF SAMPLE: BANDING

KNOWN	AM	AF	IM	IF
AM	50	2	5	3
AF	1	17	3	5
IM	5	1	61	5
IF	3	2	5	26
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

SPECIES: MALLARD

YEAR: 1980

TYPE OF SAMPLE: KNOWN CONTROL WESTERN WING BEE

KNOWN	AM	AF	IM	IF
AM	44	2	11	
AF		29		6
IM	2		48	
IF				43
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

SPECIES: BLACK DUCK

YEAR: 1978, 1979, 1980

TYPE OF SAMPLE: KNOWN CONTROL

KNOWN	AM	AF	IM	IF
AM	9		2	
AF		13	1	7
IM			42	3
IF			5	37
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

Appendix III Identification matrices obtained during this
(contd.) study

SPECIES BLACK DUCK

YEAR 1978 TO 1982

TYPE OF SAMPLE: BANDING

KNOWN AM	47	9	3	6
KNOWN AF	6	15	7	8
KNOWN IM	3	3	51	20
KNOWN IF	3	4	17	55
	AM	AF	IM	IF

RESULTING IDENTIFICATIONS

A listing of the program used to calculate age ratio estimates for the 14 models in this study. The formatting of the program has been changed to allow it to fit within the margins of this report.

```

PROGRAM RATIOS
* THIS PROGRAM WAS WRITTEN IN FORTRAN-77
* BY STEVE WENDT IN FEBRUARY 1984.
* THE PROGRAM CALCULATES ESTIMATES OF AGE RATIOS
* (IMMATURES / ADULTS) IN A DUCK POPULATION.
* THERE ARE THREE TYPES OF INPUT ACCEPTED:
* 1. CONTROL SAMPLE RESULTS. BECAUSE THE AGE
* RATIOS ARE BASED ON WING IDENTIFICATION THAT
* IS NOT WITHOUT ERROR THE RESULTS OF IDENTIFICATION
* OF KNOWN AGE AND SEX WINGS ARE USED TO CORRECT
* THE WING SAMPLE. FOR PURPOSES OF SIMULATION
* THE CONTROL SAMPLE IS ASSUMED TO BE
* MULTINOMIALLY DISTRIBUTED WITHIN EACH OF
* THE FOUR AGE/SEX CLASSES, GIVEN THE
* TOTAL NUMBER OF CONTROL WINGS IN
* EACH CATEGORY.
* 2. WING SURVEY RESULTS. THE NUMBER OF WINGS
* RECEIVED IN EACH CATEGORY OF AGE/SEX.
* SOME MODELS CALCULATE THE AGE RATIO USING
* FEMALE WINGS ONLY. THIS DATA IS REQUIRED
* FOR ALL MODELS.
* 3. BANDING RESULTS. THE NUMBER OF BANDINGS
* AND RECOVERIES IN EACH AGE/SEX CATEGORY.
* THESE DATA ARE USED TO CALCULATE THE
* RELATIVE VULNERABILITY IN SOME MODELS.
* IF INSUFFICIENT DATA ARE AVAILABLE FOR ANALYSIS BY
* SEX, ZEROES ARE ENTERED FOR FEMALE DATA.
* THE PROGRAM CALCULATES MEAN, VARIANCE, AND PERCENTILES
* (5, 95, AND 50%) FOR THE AGE RATIO BY A MONTE CARLO
* SIMULATION ACCORDING TO 14 DIFFERENT MODELS. THE
* SAME SIMULATED SAMPLES ARE USED FOR ALL ACTIVE MODELS.
* RESULTS (MEAN & VARIANCE) ARE DISPLAYED AFTER EVERY
* 100 TRIALS.
* 14 MODELS ARE INCLUDED. SOME DATA SETS ARE NOT
* APPROPRIATE FOR SOME MODELS. IF THIS IS TRUE FOR THE
* CENTRAL DATA (INPUT, RATHER THAN GENERATED), OR IF
* IT HAPPENS IN MORE THAN 10% OF THE TRIALS, THE MODEL
* IS REMOVED FROM FURTHER CONSIDERATION.
* THE FOURTEEN MODELS ARE:
*
* CONTROL SAMPLE
* CATEGORIES
* (AGE/SEX=4
* AGE=2 BANDING SEXES USED
* MODEL NOT USED=0) CATEGORIES IN RATIO
*
* 1 0 0 BOTH
* 2 0 0 FEMALE
* 3 0 2 BOTH
* 4 0 2 FEMALE
* 5 0 4 BOTH
* 6 0 4 FEMALE
* 7 2 0 BOTH
* 8 2 2 BOTH
* 9 4 0 BOTH
* 10 4 0 FEMALE
* 11 4 2 BOTH
* 12 4 2 FEMALE
* 13 4 4 BOTH
* 14 4 4 FEMALE
* VARIABLES USED
*
* CONTROL(CALLED,TRUE)-ARRAY OF CONTROL SAMPLE (AS INPUT)
* SUBSCRIPTS AM-1
* AF-2
* IM-3
* IF-4
* TRUE()-COLUMN TOTALS OF CONTROL(,). THE SIZE OF EACH

```

```

SAMPLE
* IS FIXED IN THE SIMULATIONS
*RECOVERY()-ARRAY OF RECOVERIES IN EACH CATEGORY (AS
  INPUT)
*BANDING()- " " BANDINGS " " " "
*WING()- " " WINGS " " " "
*VALID-ARRAY OF LOGICAL VARIABLES INDICATING VALIDITY OF
* THE 14 MODELS
*CONTROLS(CALLED,TRUE,1-100)-100 SIMULATED ARRAYS OF
* CONTROL SAMPLE. THIS IS ALWAYS 4 X 4.
* IF NO 4 X 4 MODELS ARE ACTIVE ALL DATA IS
* USED IN THE MALE COMPONENT.
*CONTROL4(4,4) AND CONTROL2(2,2)
* CONTROL SAMPLE ARRAYS FOR USE IN CALCULATION FOR ONE
* TRIAL. COLUMNS ARE DIVIDED BY TRUE() TO GIVE
* PROPORTIONS BEFORE INVERSION.
*C4,C2-LOGICAL VARIABLES INDICATING WHETHER ANY MODELS
  USING
* CONTROL SAMPLES OF THE INDICATED SIZE ARE ACTIVE.
*RECVS(4,100)-100 SIMULATED ARRAYS OF RECOVERIES. IF NO
  SEX-BASED
* VULNERABILITY CALCULATION IS REQUIRED ALL DATA IS IN
  THE
* MALE COMPONENT. BANDINGS ARE TAKEN TO BE FIXED AND
* RECOVERIES ARE DISTRIBUTED BINOMIALLY.
*R4,R2-LOGICAL VARIABLES INDICATING WHETHER ANY MODELS
* USING BANDING SAMPLES OF THE INDICATED SIZE ARE
  ACTIVE.
*REC4(),REC2()-PARTICULAR BAND RECOVERY ARRAYS FOR USE
  IN COMPUTING
*WINGS(4,100)-100 SIMULATED ARRAYS OF WING RECEIPTS. THE
  TOTAL
* NUMBER OF WINGS IS TAKEN AS FIXED AND SIMULATED
  SAMPLES
* ARE MULTINOMIALLY DISTRIBUTED (INTO THE 4 AGE/SEX
  CLASSES)
*WING4()-PARTICULAR ARRAY OF WING SAMPLE FOR
  CALCULATION.
*S1(14)-SUM OF X (RATIOS) FOR THE 14 MODELS.
*S2(14)-SUM OF X*X " " " "
*TRIALS(14)-COUNT OF SUCCESSFUL TRIALS FOR THE 14 MODELS.
*FAILS(14)- " " FAILED " " " "
*STEPS(3,14)-LOGICAL ARRAY DESCRIBING STEPS DONE IN
  CALCULATION FOR EACH MODEL:
* STEP 1-CONTROL SAMPLE INVERSION
* 2-VULNERABILITY CORRECTION
* 3-COMBINE SEXES FOR RATIO
*RESULTS-ARRAY OF RESULTS RETURNED FROM CALCULATION.
*FLAGS-LOGICAL ARRAY OF VALIDITY FLAGS FROM CALCULATION.
*CONDENSE(2,14)-CONDENSE CONTROL/BANDING TO 2 X 2 FOR
  EACH MODEL
* PROPCONT(4,4)-ARRAY OF INPUT CONTROL SAMPLES AS
  PROPORTIONS FOR USE AS PARAMETERS TO PROB. GENERATOR
* PROPWING(4)-ARRAY OF INPUT WING SAMPLE AS PROPORTIONS
  OF
* CORRESPONDING BANDINGS
DIMENSION PROPCONT(4,4),PROPWING(4),PROPRECV(4)
DIMENSION A(1000),STORE(14,1000)
INTEGER TOTWING,GENARRAY(100,4),GENSMALL(100)
DOUBLE PRECISION DSEED
REAL WORKARRAY(4)
INTEGER CONTROL(4,4),TRUE(4),WING(4),BANDING(4)
INTEGER RECOVERY(4),CONTROLS(4,4,100),RECVS(100,4)
INTEGER REC4(4),REC2(2),WINGS(100,4),WING4(4)
INTEGER TRIALS(14),FAILS(14)
LOGICAL VALID(14),C2,C4,R2,R4
LOGICAL STEPS(3,14),FLAGS(14),CONDENSE(2,14)
REAL CONTROL4(4,4),CONTROL2(2,2),S1(14),S2(14)
REAL RESULTS(14)
REAL MTEMP,MN
CHARACTER*3 AS(4)

```

```

DATA (AS(J),J=1,4)/'AM','AF','IM','IF'/
* INITIALIZE VARIABLES
DSEED=4892196
NSIM = 1000
NSTEPS=0
C4=R2=R4=C2=.TRUE.
10 DO 20 I=1,14
VALID(I)=.TRUE.
S1(I)=S2(I)=TRIALS(I)=FAILS(I)=0
DO 20 J=1,1000
20 STORE(I,J)=0
* ENTER CENTRAL VALUES
PRINT *, 'GIVE WING RECEIPTS'
PRINT *, AS(1),AS(2),AS(3),AS(4)
INPUT WING(1),WING(2),WING(3),WING(4)
PRINT *, 'GIVE BANDING DATA'
DO 30 I=1,4
PRINT *, AS(I), ' BANDINGS, RECOVERIES'
30 INPUT BANDING(I),RECOVERY(I)
PRINT *, 'GIVE CONTROL SAMPLE'
DO 40 I=1,4
PRINT *, AS(I), ' WINGS WERE CALLED'
40 INPUT
CONTROL(1,I),CONTROL(2,I),CONTROL(3,I),CONTROL(4,I)
*
* SET UP DESCRIPTION OF STEPS PERFORMED FOR EACH MODEL
DO 44 I=1,14
DO 44 J=1,3
44 STEPS(J,I)=.TRUE.
DO 45 I=1,6
45 STEPS(I,I)=.FALSE.
STEPS(2,1)=STEPS(2,2)=STEPS(2,7)=STEPS(2,9)=STEPS(2,10)=.FALSE.
DO 46 I=2,6,2
46 STEPS(3,I)=STEPS(3,I+8)=.FALSE.
* SET UP SIZES OF ARRAYS FOR EACH MODEL
DO 48 I=1,14
48 CONDENSE(1,I)=CONDENSE(2,I)=.FALSE.
CONDENSE(1,7)=CONDENSE(1,8)=.TRUE.
CONDENSE(2,3)=CONDENSE(2,4)=.TRUE.
CONDENSE(2,8)=CONDENSE(2,11)=CONDENSE(2,12)=.TRUE.
*
*VALIDATE CENTRAL VALUES TO MODELS
CALL VALIDATE(CONTROL,RECOVERY,WING,VALID)
*TOTAL COLUMNS OF CONTROL MATRIX
DO 50 I=1,4
TRUE(I)=0
DO 50 J=1,4
50 TRUE(I)=TRUE(I)+CONTROL(J,I)
*SET UP SAMPLES WITH CENTRAL VALUES
DO 60 I=1,4
REC4(I)=RECOVERY(I)
WING4(I)=WING(I)
DO 60 J=1,4
60 CONTROL4(I,J)=CONTROL(I,J)/FLOAT(TRUE(J))
DO 70 I=0,1
REC2(I+1)=RECOVERY(2*I+1)+RECOVERY(2*I+2)
DO 70 J=0,1
M=2*I+1
N=2*J+1
MTEMP=CONTROL(M,N)+CONTROL(M+1,N)+CONTROL(M,N+1)+CONTROL(M+1,N+1)
70 CONTROL2(I+1,J+1)=MTEMP/(TRUE(N)+TRUE(N+1))
*CALCULATE RESULTS FOR CENTRAL VALUES
CALL CALCULATE(VALID,STEPS,CONDENSE,CONTROL4,CONTROL2,
- BANDING,REC4,REC2,
-WING4,RESULTS,FLAGS,C2,C4,R2,R4)
*DISPLAY CENTRAL RESULTS
OUTPUT RESULTS OF RATIO CALCULATION FOR INPUT DATA
DO 80 I=1,14
IF(.NOT.VALID(I)) GO TO 80
IF(.NOT.FLAGS(I)) VALID(I)=.FALSE.;GO TO 80
PRINT *, MODEL ,I, ' RATIO ',RESULTS(I)
80 CONTINUE

```

```

* SET UP PROPORTIONS FOR USE IN MULTINOMIAL/BINOMIAL
CALLS
TOTWING=0
DO 320 I=1,4
320 TOTWING=TOTWING+WING(I)
DO 330 I=1,4
330 PROPWING(I)=FLOAT(WING(I))/TOTWING
DO 340 I=1,4
340 PROPREC(V(I)=FLOAT(RECOVERY(I))/BANDING(I)
DO 350 I=1,4
DO 350 J=1,4
350 PROPCONT(I,J)=FLOAT(CONTROL(I,J))/TRUE(J)
C4=R2-R4-C2=.FALSE.
DO 77 M=1,14
IF(VALID(M).AND.STEPS(1,M)) THEN
IF (CONDENSE(1,M)) THEN
C2=.TRUE.
ELSE
C4=.TRUE.
ENDIF
ENDIF
IF(VALID(M).AND.STEPS(2,M)) THEN
IF (CONDENSE(2,M)) THEN
R2=.TRUE.
ELSE
R4=.TRUE.
ENDIF
ENDIF
77 CONTINUE
*ITERATIVE STEP FOR GENERATED TRIALS
100 IF(NSTEPS.GE.NSIM) GO TO 200
CALL GGMTN(DSEED,100,TOTWING,4,PROPWING,100,WINGS)
IF(.NOT.(C4.OR.C2)) GO TO 489
DO 109 J=1,4
DO 108 I=1,4
108 WORKARRAY(I)=PROPCONT(I,J)
CALL GGMTN(DSEED,100,TRUE(J),4,WORKARRAY,100,GENARRAY)
DO 109 I=1,4
DO 109 K=1,100
109 CONTROLS(I,J,K)=GENARRAY(K,I)
489 IF(.NOT.(R4.OR.R2)) GO TO 692
DO 110 I=1,4
CALL GGBN(DSEED,100,BANDING(I),PROPREC(V(I),GENSMALL)
DO 110 J=1,100
110 REC(VS(J,I)=GENSMALL(J)
692 DO 199 NCASE=1,100
DO 130 I=1,4
REC4(I)=REC(VS(NCASE,I)
WING4(I)=WINGS(NCASE,I)
DO 130 J=1,4
130 CONTROL4(I,J)=FLOAT(CONTROLS(I,J,NCASE))/TRUE(J)
DO 140 I=0,1
REC2(I+1)=REC4(2*I+1)+REC4(2*I+2)
DO 140 J=0,1
M=2*I+1
N=2*J+1
MTEMP=CONTROLS(M,N,NCASE)+CONTROLS(M+1,N,NCASE)
MTEMP=MTEMP+CONTROLS(M,N+1,NCASE)+CONTROLS(M+1,N+1,NCASE)
140 CONTROL2(I+1,J+1)=MTEMP/(TRUE(N)+TRUE(N+1))
*CALCULATE RESULT FOR SIMULATED VALUES
CALL CALCULATE(VALID,STEPS,CONDENSE,CONTROL4,CONTROL2,
-BANDING,REC4,REC2,WING4,RESULTS,FLAGS,C2,C4,R2,R4)
DO 150 I=1,14
IF(.NOT.VALID(I)) GO TO 150
IF(.NOT.FLAGS(I)) FAILS(I)=FAILS(I)+1;GO TO 150
S1(I)=S1(I)+RESULTS(I)
S2(I)=S2(I)+(RESULTS(I))**2
TRIALS(I)=TRIALS(I)+1
STORE(I,TRIALS(I))-RESULTS(I)
150 CONTINUE
NSTEPS=NSTEPS+1
199 CONTINUE

```

```

DO 678 I=1,14
678
IF((FLOAT(FAILS(I))/TRIALS(I)).GT.0.2)VALID(I)=.FALSE.
GO TO 100
*DISPLAY RESULTS
200 PRINT *, 'RESULTS'
DO 225 I=1,14
IF (.NOT.VALID(I)) GO TO 225
PRINT *, MODEL , I, TRIALS , TRIALS(I), FAILS
      FAILS(I)
IF(TRIALS(I).LT.2) GO TO 225
VARIANCE=S2(I)-(S1(I)**2)/TRIALS(I)
VARIANCE=VARIANCE/(TRIALS(I)-1)
MN=S1(I)/TRIALS(I)
SD=VARIANCE**.5
PRINT *, VARIANCE , VARIANCE, SD ,SD, CV 'eSD/MN
NCTR=TRIALS(I)
DO 323 J=1,NCTR
323 A(J)=STORE(I,J)
CALL VSRTA(A,NCTR)
PRINT *, RANGE , A(1),A(NCTR*.5),A(NCTR)
PRINT *, MEAN , S1(I)/TRIALS(I)
PRINT *, 5% , A(NCTR*.05), 95% , A(NCTR*.95)
225 CONTINUE
STOP
END
SUBROUTINE VALIDATE (CONTROL4,REC4,WING,MODEL)
*RETURNS A LOGICAL ARRAY OF MODEL VALIDITY
INTEGER CONTROL4(4,4),REC4(4),ADULT,IMM,WING(4)
LOGICAL FOURC,TWOC,FOURR,TWOR,MODEL(14),SEX
SEX=FOURC=TWOC=FOURR=TWOR=.TRUE.
DO 5 I=1,14
5 MODEL(I)=.TRUE.
DO 10 I=1,14
IF (REC4(I).EQ.0) FOURR=.FALSE.
10 IF (CONTROL4(I,I).EQ.0) FOURC=.FALSE.
IF (FOURR) GO TO 20
ADULT = REC4(1)+REC4(2)
IMM = REC4(3)+REC4(4)
IF ((ADULT.EQ.0).OR.(IMM.EQ.0)) TWOR=.FALSE.
20 IF (FOURC) GO TO 30
ADULT=CONTROL4(1,1)+CONTROL4(2,2)
IMM=CONTROL4(3,3)+CONTROL4(4,4)
IF ((ADULT.EQ.0).OR.(IMM.EQ.0)) TWOC=.FALSE.
30 ADULT=WING(2)
IMM=WING(4)
IF ((ADULT.EQ.0).OR.(IMM.EQ.0)) SEX=.FALSE.
MODEL(14)=FOURC.AND.FOURR.AND.SEX
MODEL(13)=FOURC.AND.FOURR
MODEL(12)=FOURC.AND.TWOR.AND.SEX
MODEL(11)=FOURC.AND.TWOR
MODEL(10)=FOURC.AND.SEX
MODEL(9)=FOURC
MODEL(8)=TWOC.AND.TWOR
MODEL(7)=TWOC
MODEL(6)=FOURR.AND.SEX
MODEL(5)=FOURR
MODEL(4)=TWOR.AND.SEX
MODEL(3)=TWOR
MODEL(2)=SEX
MODEL(1)=.TRUE.
END
SUBROUTINE CALCULATE(MODELS,STEPS,CONDENSE,CONT4,
-CONT2,BAND,REC4,REC2,WING,RESULT,F,C2,C4,R2,R4)
*SETS UP CALL TO FUNCTION RATIO FOR ALL 14 MODELS
LOGICAL MODELS(14),F(14),STEP1,STEP2,STEP3
LOGICAL STEPS(3,14),CONDENSE(2,14),C4,C2,R2,R4
REAL CONT4(4,4),CONT2(2,2),RESULT(14)
INTEGER REC4(4),REC2(2),WING(4),BAND(4)
DO 77 M=1,14
F(M)=MODELS(M)
77 CONTINUE

```

```

STEP1=.TRUE.
*CONDITIONALLY COMPILED SECTION FOR CHECKOUT
X DO 99 I=1,4
X99 PRINT *, (CONT4(I,J),J=1,4)
X DO 98 I=1,4
X 98 PRINT *, I, BAND(I),WING(I)
X DO 97 I=1,4
X97 PRINT *, I, REC4(I)
IF (C4) CALL INVERT (CONT4,4,STEP1)
IF (.NOT.STEP1)
    F(9)=F(10)=F(11)=F(12)=F(13)=F(14)=.FALSE.
STEP1=.TRUE.
IF (C2) CALL INVERT(CONT2,2,STEP1)
IF (.NOT.STEP1) F(7)=F(8)=.FALSE.
DO 10 M=1,14
IF (.NOT.F(M)) GO TO 10
STEP1=STEPS(1,M)
STEP2=STEPS(2,M)
STEP3=STEPS(3,M)
X PRINT *, M, 'MODEL'
IF(CONDENSE(1,M).AND.CONDENSE(2,M)) THEN
R=RATIO(2,2,CONT2,BAND,REC2,WING,STEP1,STEP2,STEP3)
ELSE IF (CONDENSE(1,M)) THEN
R=RATIO(2,4,CONT2,BAND,REC4,WING,STEP1,STEP2,STEP3)
ELSE IF (CONDENSE(2,M)) THEN
R=RATIO(4,2,CONT4,BAND,REC2,WING,STEP1,STEP2,STEP3)
ELSE
R=RATIO(4,4,CONT4,BAND,REC4,WING,STEP1,STEP2,STEP3)
ENDIF
X PRINT *, R
IF(R.LT.0.01) F(M)=.FALSE.;GO TO 10
IF (R.GT.12) F(M)=.FALSE.;GO TO 10
F(M)=.TRUE.
RESULT(M)=R
10 CONTINUE
END
FUNCTION
    RATIO(N,M,CONTROL,BAND,RECOV,WING,STEP1,STEP2,STEP3)
INTEGER N,M,BAND(4),RECOV(M),WING(4)
REAL CONTROL(N,N),NEWWINGS(4),NEWBAND(4)
REAL PRODUCT(4),ADULTS,IMMATURES
LOGICAL STEP1,STEP2,STEP3
DO 10 I=1,4
NEWBAND(I)=BAND(I)
10 NEWWINGS(I)=WING(I)
IF(N.EQ.2) NEWWINGS(1)=WING(1)+WING(2);
- NEWWINGS(2)=WING(3)+WING(4)
IF(M.EQ.2)
    NEWBAND(1)=BAND(1)+BAND(2);NEWBAND(2)=BAND(3)+
- BAND(4)
IF (STEP1) THEN
CALL VMULFF(CONTROL,NEWWINGS,N,N,1,N,4,PRODUCT,
- 4,IER)
IF(IER.EQ.129) OUTPUT 'PROGRAM ERROR'
X PRINT *, 'NEW ',(PRODUCT(I),I=1,4)
DO 20 I=1,4
20 NEWWINGS(I)=PRODUCT(I)
ENDIF
IF (STEP2) THEN
DO 30 I=1,M
IF (RECOV(I).EQ.0) RATIO=0;RETURN
*****MODELS WITH CONDENSED BANDINGS BUT FULL WING ARRAY
*****NEED SPECIAL TREATMENT HERE
V=NEWBAND(I)/RECOV(I)
IF(N.EQ.M) GO TO 29
*HERE M=2 AND N=4
NEWWINGS(2*I-1)=NEWWINGS(2*I-1)*V
NEWWINGS(2*I)=NEWWINGS(2*I)*V
GO TO 30
29 NEWWINGS(I)=NEWWINGS(I)*V
30 CONTINUE
*
```

```

ENDIF
IF (N.EQ.2) THEN
ADULTS=NEWWINGS(1)
IMMATURES=NEWWINGS(2)
ELSE IF (STEP3) THEN
IMMATURES=NEWWINGS(3)+NEWWINGS(4)
ADULTS=NEWWINGS(1)+NEWWINGS(2)
ELSE
IMMATURES=NEWWINGS(4)
ADULTS=NEWWINGS(2)
ENDIF
IF(ADULTS.LT.0.01) RATIO=0; RETURN
RATIO = IMMATURES/ADULTS
RETURN
END
SUBROUTINE INVERT (INPLACE,SIZE,FLAG)
*THIS ROUTINE DOES A JORDAN/GAUSS ELIMINATION TO INVERT
  A
*MATRIX. THE INVERTED MATRIX REPLACES THE ORIGINAL.
*ONLY MATRICES UP TO DIMENSION 4 X 4 ARE ALLOWED.
INTEGER SIZE,ROW,COLUMN,PIVOT
REAL INPLACE(SIZE,SIZE),WORK(4,8),PIV
LOGICAL FLAG
FLAG=.TRUE.
IF(SIZE.GT.4) OUTPUT 'DIMENSION
  ERROR'; FLAG=.FALSE.; RETURN
DO 10 ROW=1,SIZE
DO 10 COLUMN=1,SIZE
WORK(ROW,COLUMN)=INPLACE(ROW,COLUMN)
IF(ROW.EQ.COLUMN) THEN
WORK(ROW,COLUMN+SIZE)=1.0
ELSE
WORK(ROW,COLUMN+SIZE)=0.0
ENDIF
10 CONTINUE
DO 20 PIVOT=1,SIZE
PIV=WORK(PIVOT,PIVOT)
IF(ABS(PIV).GT.1E-50) GO TO 30
DO 40 M=(PIVOT+1),SIZE
40 IF (ABS(WORK(M,PIVOT)).GT.1E-50) GO TO 50
FLAG=.FALSE.
RETURN
50 PIV=WORK(M,PIVOT)
DO 60 J=1,SIZE*2
X=WORK(M,J)
WORK(M,J)=WORK(PIVOT,J)
60 WORK(PIVOT,J)=X
30 DO 70 COLUMN=PIVOT,2*SIZE
70 WORK(PIVOT,COLUMN)=WORK(PIVOT,COLUMN)/PIV
DO 80 J=1,SIZE
IF (.NOT.(J.EQ.PIVOT)) THEN
PIV=WORK(J,PIVOT)
DO 90 COLUMN=1,SIZE*2
90 WORK(J,COLUMN)=WORK(J,COLUMN)-PIV*WORK(PIVOT,COLUMN)
ENDIF
80 CONTINUE
20 CONTINUE
DO 100 ROW=1,SIZE
DO 100 COLUMN=1,SIZE
100 INPLACE(ROW,COLUMN)=WORK(ROW,COLUMN+SIZE)
RETURN
END

```

Appendix VAdditional estimates of sex ratios

Using the method of Chapter 5 additional estimates of sex ratio were calculated. They are shown here with their standard errors.

Model	Green-winged teal	Canvasback	American wigeon	Gadwall
1	.71 $\pm$ 0.05	1.32 $\pm$ 0.06	.96 $\pm$ 0.07	1.06 $\pm$ 0.07
2*	.52 $\pm$ 0.10	1.36 $\pm$ 0.13	.91 $\pm$ 0.15	1.71 $\pm$ 0.23
3	2.04 $\pm$ 0.99	.67 $\pm$ 0.07	1.29 $\pm$ 0.47	.66 $\pm$ 0.17
4*	1.49 $\pm$ 0.80	.69 $\pm$ 0.10	1.23 $\pm$ 0.48	1.06 $\pm$ 0.30
5	2.14 $\pm$ 1.21	.88 $\pm$ 0.11	-	.91 $\pm$ 0.42
6*	1.48 $\pm$ 1.35	.30 $\pm$ 0.06	-	1.78 $\pm$ 1.23
7	.57 $\pm$ 0.09	1.32 $\pm$ 0.06	1.07 $\pm$ 0.15	1.17 $\pm$ 0.42
8*	1.64 $\pm$ 0.82	.67 $\pm$ 0.07	1.45 $\pm$ 0.55	.73 $\pm$ 0.40
9	.62 $\pm$ 0.10	-	1.17 $\pm$ 0.28	-
10*	-	-	-	-
11	1.77 $\pm$ 0.88	-	1.58 $\pm$ 0.68	-
12*	-	-	-	-
13	1.81 $\pm$ 1.15	-	-	-
14*	-	-	-	-

* shows those models that estimate the adult sex ratio

Appendix VIDevelopment of an index to allow comparison with
waterfowl production surveys

Most of the prairie and parkland breeding area in western Canada is included in surveys in July to determine the production of young ducks. The survey methodology is described in Henny et al. (1972). This survey does not directly estimate the number of young produced, but instead a combination of three indices, for brood production, brood size, and late nesting. The survey does not distinguish broods by species.

In order to make a comparison of these survey results with age ratios calculated from wings, a production index was calculated. Five subregions of the survey area were used; southern Alberta, northern Manitoba and Saskatchewan, southern Saskatchewan, southern Manitoba, and northern Alberta with part of the Northwest Territories. Following Henny et al., the mean brood size in each region was computed by weighting individual stratum means by the brood index. Then for each region a production index was calculated as:

$$R_{\text{prod}} = B * (BI + L) / D$$

where B is the mean brood size seen in the survey

BI is the brood index

L is the late nesting index and

D is the estimate of breeding populations from the May breeding ground surveys.

The production index for western Canada was obtained as a weighted mean of the regional indices, weighting by the breeding duck population, D, in each region.

The July survey indices were taken from Henny et al. (1972), and from various U.S. Fish and Wildlife Service Waterfowl Status Reports. R. Pospahala provided a few missing data in a personal communication.

Appendix VII

The assumption of a simple random sample of wings causes an underestimation of variance

In the models described in this thesis it is assumed that, from a given species, the wings received are a simple random sample of the birds killed by hunters. This is a simplification because the wing survey is based on a selection of hunters, not wings. A simple random sample of hunters produces a cluster sample of wings (Cochran, 1977).

The analysis of age ratios is independent among the species studied. In effect the wings make up many surveys, each a cluster sample for the proportion of immatures in one of the species.

If the hunters themselves sampled the birds in a random way the assumption of simple random sampling would be justified. If there is a tendency for individual hunters to have little age variation in the birds they have killed, however, then several wings from one hunter would not provide as much information as the same number of wings, one each from different hunters.

Cochran (1977, p.247) gives an expression for the ratio of the variances calculated i) from a cluster sample, and ii) from the simple random sample, ignoring clusters, when sampling for the proportion, p :

$$\frac{V_{\text{cluster}}(p)}{V_{\text{s.r.s.}}} = \frac{\sum_{i=1}^M (p_i - P)^2}{N M P Q} \quad (36)$$

V
s.r.s.

N M P Q

where, in our case, P is the mean of the p_i , over clusters $Q = 1 - P$, p_i is the proportion for each cluster (hunter) M_i is the number of wings from each hunter N is the number of hunters and the summation is over clusters

Not all hunters who respond to the survey give a valid hunting permit number, so the estimation for formula (36) must be restricted to those who do. This allows the different hunters to be distinguished. To show the importance of cluster sampling, one year (1979) was chosen. The calculation of equation 36 was performed both for model R. (all wings, table 40) and model F (female wings, table 41). The tables show all species for which 50 or more wings were received in each region.

In the tables, the design effect shows the importance of cluster sampling to the estimates of proportion of immatures of each species. One interpretation is that the design effect is the factor that the sample size (of wings) should be multiplied by so that the cluster sample will give the variance now apparent when the clusters are ignored. From this point of view design effects of 4 and greater can be interpreted as serious indications that the cluster design is important.

There is another aspect of the cluster sampling design that is important. This is the method of estimation of P . In the simple design P is estimated by the overall proportion of immatures. In the cluster design, P is estimated as the mean of the proportions of immatures, averaged over all the hunters. In the extreme cases where each hunter sends only one wing, or where there is only one hunter, both methods give the same result. Otherwise there can be a difference between the two

methods. Table 42 compares the proportions, P from table 40 with the proportions calculated as if the sample were simple. The effect that this has on the age ratio is calculated, using equation (1).

From these tables it is clear that the cluster effect is important for some species in some regions. The estimates of variance presented in this report may be underestimates for these species. Further, cluster sampling may produce a bias in the estimate of R by the methods used here, causing larger values of R in most cases. The extent of this bias cannot be taken from table 42 directly, but should be investigated further by a division of this survey into strata.

The wing survey was originally designed with several hunter categories that might have been used for an analysis of the results according to strata. The survey packages sent to hunters were prenumbered to allow identification. It was found that a number of hunters gave their packages to friends, and the survey processing failed to match prenumbered envelopes to the sample selection. Because of this, and to save expense, the prenumbered envelopes were discontinued in 1972. This has prevented analysis according to the stratified, cluster sampling design.

In 1984 a new procedure for identifying envelopes with gummed labels was initiated. This will allow an analysis by clusters within the survey strata to begin in 1985.

The female age ratio methods show less effect from the cluster sampling method. This is another reason in favour of these methods (those with the letter 'F' in their names).

Table 40. Design effect due to cluster sampling for the proportion of immatures, P.

1979 - male and female wings

Region	Species	Design Effect	P	Wings	Hunters
Maritime	Common Merganser	2.951	0.77	50	31
	Mallard	1.272	0.69	62	52
	Black Duck	6.581	0.75	1375	569
	American Wigeon	11.132	0.82	60	39
	Green-winged Teal	6.826	0.78	497	251
	Blue-winged Teal	2.631	0.62	267	147
	Wood Duck	1.661	0.58	62	48
	Ring-necked Duck	4.621	0.76	224	123
	Common Goldeneye	5.120	0.58	170	79
	Oldsquaw	2.819	0.48	57	27
	Common Eider	2.878	0.41	90	37
Ontario and Quebec	Common Merganser	2.061	0.63	73	51
	Hooded Merganser	3.873	0.72	203	136
	Mallard	9.298	0.74	2554	1129
	Black Duck	5.587	0.82	1481	801
	Gadwall	1.964	0.75	117	91
	American Wigeon	2.531	0.80	283	198
	Green-winged Teal	4.352	0.81	532	329
	Blue-winged Teal	2.486	0.73	436	301
	Pintail	4.434	0.83	188	141
	Wood Duck	2.552	0.56	895	522
	Redhead	4.068	0.71	214	116
	Canvasback	3.451	0.73	96	56
	Greater Scaup	3.535	0.60	212	120
	Lesser Scaup	3.523	0.59	286	153
	Ring-necked Duck	6.967	0.75	619	317

Table 40. Design effect due to cluster sampling for the
 (contd.) proportion of immatures, P.

1979 - male and female wings

Region	Species	Design Effect	P	Wings	Hunters
	Common Goldeneye	7.958	0.66	308	167
	Bufflehead	4.242	0.45	228	105
	Black Scoter	1.966	0.42	53	33
	White-w. Scoter	1.800	0.80	60	45
	Surf Scoter	7.491	0.79	109	57
Prairies	Mallard	5.728	0.40	3873	1010
	Gadwall	5.723	0.76	315	189
	American Wigeon	2.193	0.88	197	145
	Green-winged Teal	9.616	0.80	144	87
	Blue-winged Teal	4.414	0.72	236	127
	Shoveler	4.291	0.86	183	106
	Pintail	4.276	0.81	363	235
	Redhead	2.398	0.86	119	87
	Canvasback	2.221	0.87	85	67
	Lesser Scaup	2.837	0.55	111	69
	Ring-necked Duck	2.769	0.85	79	40

Table 41. Design effect due to cluster sampling for the proportion of immatures, P.

1979 - female wings only

Region	Species	Design Effect	P	Wings	Hunters
Maritime	Black Duck	4.144	0.81	708	409
	Green-winged Teal	3.345	0.75	238	157
	Blue-winged Teal	1.973	0.68	155	111
	Ring-necked Duck	3.340	0.82	117	84
	Common Goldeneye	3.458	0.64	80	50
Ontario and Quebec	Mallard	5.166	0.74	1166	686
	Black Duck	2.393	0.84	697	487
	Gadwall	1.585	0.74	69	57
	American Wigeon	1.754	0.85	140	114
	Green-winged Teal	3.258	0.77	277	197
	Blue-winged Teal	1.678	0.76	215	179
	Pintail	2.126	0.76	100	80
	Wood Duck	1.967	0.67	385	277
	Redhead	2.766	0.75	114	76
	Greater Scaup	2.127	0.54	85	59
	Lesser Scaup	2.235	0.67	113	78
	Ring-necked Duck	4.110	0.79	332	206
	Common Goldeneye	4.205	0.76	119	90
	Bufflehead	3.229	0.66	99	62
Prairies	Mallard	4.164	0.57	1617	732
	Gadwall	4.019	0.85	162	116
	American Wigeon	1.247	0.86	95	79
	Green-winged Teal	5.937	0.79	76	53
	Blue-winged Teal	2.491	0.72	112	80
	Shoveler	1.358	0.87	87	64
	Pintail	2.503	0.78	208	148
	Redhead	3.301	0.88	53	43

Table 42. Comparison of age ratios calculated from identified hunters, using cluster sample and simple sample methods

1979 - male and female wings

Region	Species	P	P	R	R
		cluster	simple	cluster	simple
Maritime	Common Merganser	0.77	0.82	3.3	4.5
	Mallard	0.69	0.74	2.2	2.8
	Black Duck	0.75	0.86	3.0	6.1
	American Wigeon	0.82	0.80	4.6	4.0
	Green-winged Teal	0.78	0.87	3.5	6.7
	Blue-winged Teal	0.62	0.74	1.6	2.8
	Wood Duck	0.58	0.69	1.4	2.2
	Ring-necked Duck	0.76	0.81	3.2	4.3
	Common Goldeneye	0.58	0.69	1.4	2.2
	Oldsquaw	0.48	0.49	0.9	1.0
	Common Eider	0.41	0.54	0.7	1.2
Ontario and Quebec	Common Merganser	0.63	0.71	1.7	2.4
	Hooded Merganser	0.72	0.78	2.6	3.5
	Mallard	0.74	0.85	2.8	5.7
	Black Duck	0.82	0.88	4.6	7.3
	Gadwall	0.75	0.80	3.0	4.0
	American Wigeon	0.80	0.84	4.0	5.2
	Green-winged Teal	0.81	0.86	4.3	6.1
	Blue-winged Teal	0.73	0.80	2.7	4.0
	Pintail	0.83	0.83	4.9	4.9
	Wood Duck	0.56	0.68	1.3	2.1
	Redhead	0.71	0.83	2.4	4.9
	Canvasback	0.73	0.82	2.7	4.6

Table 42. Comparison of age ratios calculated from identified
 (cont.) hunters, using cluster sample and simple sample
methods

1979 - male and female wings

Region	Species	P	P	R	R
		cluster	simple	cluster	simple
	Greater Scaup	0.60	0.74	1.5	2.8
	Lesser Scaup	0.59	0.73	1.4	2.7
	Ring-necked Duck	0.75	0.83	3.0	4.9
	Common Goldeneye	0.66	0.65	1.9	1.9
	Bufflehead	0.45	0.60	0.8	1.5
	Black Scoter	0.42	0.45	0.7	0.8
	White-w. Scoter	0.80	0.83	4.0	4.9
	Surf Scoter	0.79	0.83	3.8	4.9
Prairies	Mallard	0.40	0.66	0.7	1.9
	Gadwall	0.76	0.82	3.2	4.6
	American Wigeon	0.88	0.90	7.3	9.0
	Green-winged Teal	0.80	0.87	4.0	6.7
	Blue-winged Teal	0.72	0.82	2.6	4.6
	Shoveler	0.86	0.89	6.1	8.1
	Pintail	0.81	0.87	4.3	6.7
	Redhead	0.86	0.91	6.1	10.1
	Canvasback	0.87	0.91	6.7	10.1
	Lesser Scaup	0.55	0.66	1.2	1.9
	Ring-necked Duck	0.85	0.94	5.7	15.7

Appendix VIIIScientific names of species of duck

<u>Code</u> *	<u>Common name</u>	<u>Scientific name</u>
A	Wood duck	<i>Aix sponsa</i>
B	American wigeon	<i>Anas americana</i>
C	Gadwall	<i>Anas strepera</i>
D	Green-winged teal	<i>Anas crecca</i>
E	Mallard	<i>Anas platyrhynchos</i>
F	Black duck	<i>Anas rubripes</i>
G	Pintail	<i>Anas acuta</i>
H	Blue-winged teal	<i>Anas discors</i>
I	Shoveler	<i>Anas clypeata</i>
J	Canvasback	<i>Aythya valisineria</i>
K	Redhead	<i>Aythya americana</i>
L	Ring-necked duck	<i>Aythya collaris</i>
M	Greater scaup	<i>Aythya marila</i>
N	Lesser scaup	<i>Aythya affinis</i>
O	Common eider	<i>Somateria mollissima</i>
P	Oldsquaw	<i>Clangula hyemalis</i>
Q	Black scoter	<i>Melanitta nigra</i>
R	White-winged scoter	<i>Melanitta fusca</i>
S	Surf scoter	<i>Melanitta</i> <i>perapicillata</i>
T	Bufflehead	<i>Bucephala albeola</i>
U	Barrow's goldeneye	<i>Bucephala islandica</i>
V	Common goldeneye	<i>Bucephala clangula</i>
W	Hooded merganser	<i>Lophodytes cucullatus</i>
X	Red-breasted merganser	<i>Mergus serrator</i>
Y	Common merganser	<i>Mergus merganser</i>

*codes used in Figure 65

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