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AN ANALYSIS OF A MEASURE OF PRODUCTIVITY  
IN MULE DEER POPULATIONS

by  
Ronald J. Rye1

A thesis submitted in partial fulfillment  
of the requirements for the degree

of  
MASTER OF SCIENCE  
in  
Wildlife Ecology

UTAH STATE UNIVERSITY  
Logan, Utah

1980

## ACKNOWLEDGEMENTS

This research was initially funded by the Utah Division of Wildlife Resources through the Co-op Wildlife Research Unit at Utah State University. I am most grateful to Dr. Fredrick G. Lindsey, Assistant Director of the Co-op Unit, for definition of the problem, helpful insights and guidance in this research effort.

A portion of the computer funds for this project were provided by the College of Natural Resources. I would like to thank Dr. Thadis W. Box, Dean of the College of Natural Resources, for authorizing the use of these funds.

I would also like to thank Dr. John A. Kadlec for his critical review of the thesis and for assuming the responsibilities as Chairman of my Graduate Committee upon the departure of Dr. Charles W. Fowler; Dr. H. Charles Romesburg of my Graduate Committee for his helpful suggestions and philosophical insights; and Dr. George S. Innis for his critical review of the thesis and suggestions.

The contributions provided by my original advisor and Graduate Committee member, Dr. Charles W. Fowler, are especially acknowledged. Much of the success of my graduate program was due to his helpful and patient guidance. Also, I am most grateful for the many hours we spent interacting.

Finally, I am deeply appreciative of the support and encouragement extended by Jane Carla Wipf.

Ronald J. Ryel

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## ABSTRACT

An Analysis of a Measure of Productivity  
in Mule Deer Populations

by

Ronald J. Ryel, Master of Science

Utah State University, 1980

Major Professor: Dr. John A. Kadlec  
Department: Wildlife Science

The purpose of this study was to investigate the relationship between the fall proportion of fawns among fawns and does in a mule deer population and two measures of productivity, the spring recruitment rate and the reproductive performance as measured in the fall. The spring recruitment rate was defined to be the number of fawns per doe which were recruited into the population at 1 year of age. The reproductive performance was defined to be the number of fawns produced per doe 2 years or older which survive to a specified time. The relationships between these quantities were measured by calculating linear coefficients of correlation from data generated by a projection matrix model of a mule deer population. A coefficient of correlation of 0.86 was found between the fall proportion of fawns and the rate at which fawns are recruited into the spring population. A coefficient of correlation of 0.89 was found between the fall proportion of fawns and the reproductive performance as measured in the fall.

The effect of misclassifying fawns as does and does as fawns on estimates of the proportion of fawns among fawns and does was also

investigated. A comparison was made between the expected values of two estimates of the fall proportion, one with misclassification and one without misclassification. The misclassification of fawns and does was found to bias estimates of the proportion of fawns. The bias was found to be a function of the amount of misclassification and the actual proportion of fawns.

(102 pages)

## INTRODUCTION

An important component of big game management in the western United States is the management of populations of mule deer (Odocoileus hemionus). To better understand the dynamics of these populations, game managers often collect data concerning the composition of herds by age and sex. These data are generally collected through the classification of a sample of the individuals in a herd according to age and sex, usually during the late summer and fall.

A widely used relationship stemming from the classification of individuals in a herd of deer is the relationship between the number of fawns and the number of does. This relationship is commonly expressed as the ratio of the number of fawns to the number of does. Alternatively, it may be expressed as the number of fawns per 100 does, or the proportion of fawns in the population of fawns and does ( $\text{fawns}/[\text{fawns} + \text{does}]$ ) (Leopold, 1933; Kelker, 1947; Paulik and Robson, 1969). The young-of-the-year of both sexes are classified as fawns, while females of age one or greater are typically classified as does in the classification of herds of mule deer (Wyoming Game and Fish Dept., 1977).

Although it can be expressed in various ways, the relationship between the number of fawns and does in a population is best expressed as the proportion of fawns from a statistical standpoint. Sampling errors of estimation are more readily calculated when the relationship is expressed as a proportion (Paulik and Robson, 1969; Seber, 1973). The monotonic relationship between the ratio of fawns to does and the

proportion of fawns is shown in Figure 1. Unless otherwise indicated, the proportion of fawns in the population of fawns and does will be referred to as the proportion of fawns in this work.

### Misclassification

The proportion of fawns in a population have been used in the estimation of several population attributes (Seber, 1973). As with any measured quantity utilized as an estimator, accurate statistics are desired for estimating parameters that characterize populations of mule deer. Ideally, these statistics should be unbiased and should produce estimates with small variance from sample sizes that are feasible. Similarly, sampling schemes should not greatly affect the estimates of these parameters through bias.

If all the fawns and does in a given population could be counted, unbiased and errorless values for the proportion of fawns could be calculated. However, this is rarely the case as only a portion of the total number of fawns and does are usually observed. Samples to determine the relationship between the number of fawns and number of does are typically taken using binomial sampling. This is sampling wherein  $n$  animals are counted with replacement (each animal may be counted more than once). Each individual has an equal probability of being observed. Using this type of sampling, estimates ( $\hat{P}$ ) of the proportion of fawns ( $P$ ) can be expressed simply as:

$$\hat{P} = f/n$$

where  $f$  is the number of fawns observed in a sample of fawns and does of size  $n$  (Seber, 1973).

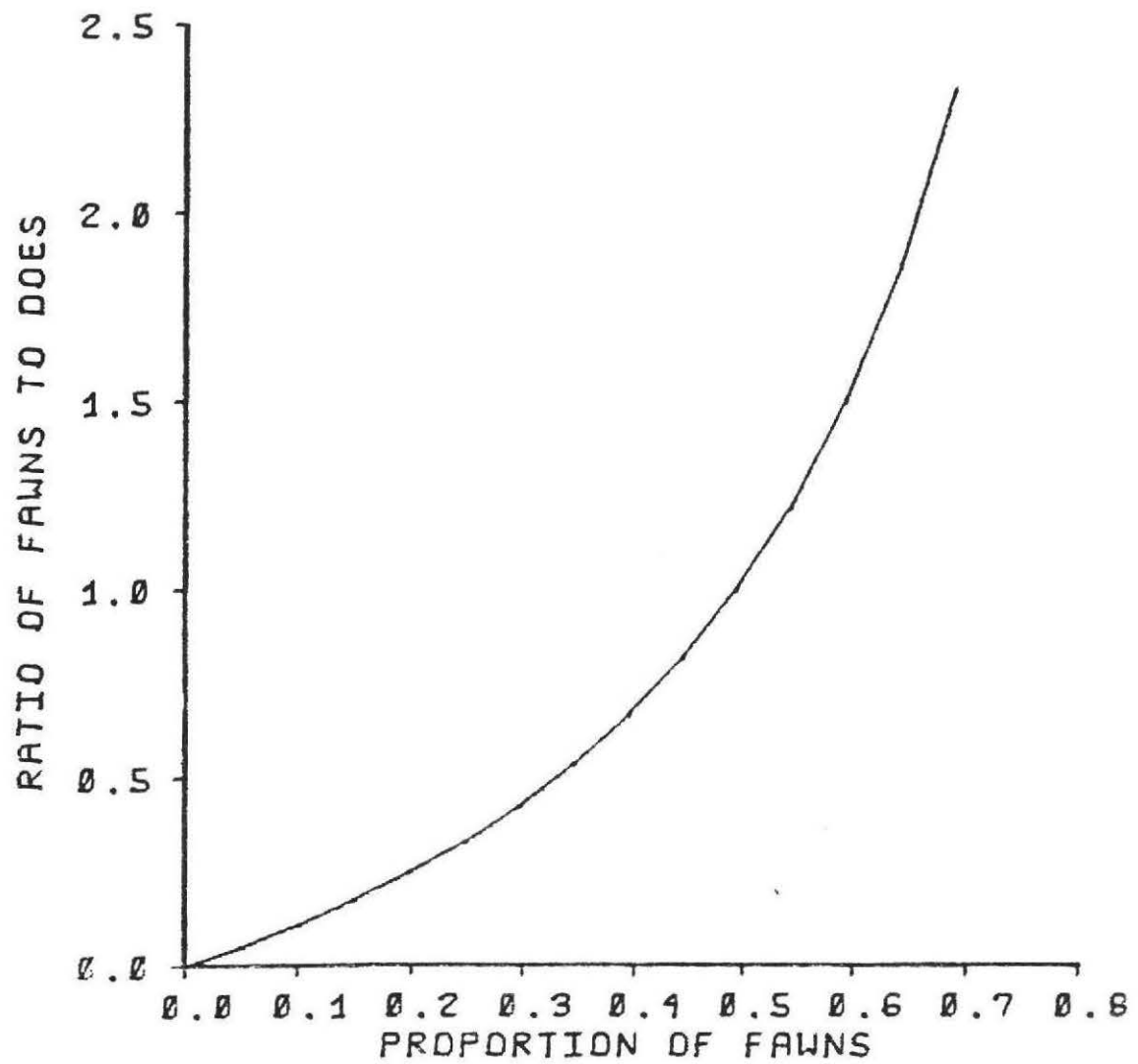


Figure 1. Relationship between the proportion of fawns (fawns/[fawns + does]) and the ratio of fawns to does (fawns/does).

If all the assumptions of binomial sampling are met, then  $\hat{P}$  is an unbiased estimate of  $P$ . However, at least two sources of bias affecting  $\hat{P}$  have been suggested. The first source involves the randomness of the sample. For  $\hat{P}$  to be unbiased, all fawns and does must have an equal probability of being counted (Hanson, 1963). A second source of bias may come from the misclassification of individuals, some fawns may be classified as does while some does may be classified as fawns (Leopold, 1933; G. H. Kelker as quoted in Hazzard, 1958; Downing, 1970; Wyoming Game and Fish Dept., 1977).

#### Productivity

The proportion of fawns or the ratio of fawns to does in a population have also been used as indices for a few population attributes. As with estimators, quantities which can be utilized as reliable indices are desired. Useful indices are those which can consistently distinguish between various values of a parameter characteristic of a population. Among Cervids in general, the abundance of young in a population is often considered to be the best indicator of herd productivity (Pimlott, 1959). The ratio of fawns to does or the proportion of fawns estimated in the fall is used extensively to monitor the productivity of herds of deer over time (Zwank, 1976).

The productivity of a herd, as this term is generally used, relates to how fast a population is growing or how rapidly it is producing a surplus of individuals for harvest. It is a relative term, is not well defined in most applications, and does not lend itself to direct measurement. The productivity of a herd may, however, be clearly expressed in terms of several useful quantities including the

rate of recruitment of individuals into the breeding population, the reproductive rate of specific components of a population and the rate of increase of a population.

Recruitment is the addition by reproduction of individuals to a portion of the population (Ricklefs, 1973). The recruitment of individuals into the breeding population is an important characteristic concerning the dynamics of a population and a useful measure of productivity. In mule deer, this occurs at about 1 year of age when most of the individuals become sexually mature and when the rate of survival begins to approach that of older ages (Robinette and Gashwiler, 1950; Robinette et al., 1977; Zwank, 1978; Medin and Anderson, 1979).

One measure of the rate at which individuals are recruited into the breeding population would be the number of fawns per doe which reach 1 year of age. Because of the relationship illustrated in Figure 1, estimates of the proportion of fawns in the spring when the fawns are 1 year old will be a consistent indicator of productivity of a population as measured by the rate at which fawns are recruited into the breeding population. Composition counts to measure productivity, however, are usually done in the fall (Wyoming Game and Fish Dept., 1977; Zwank, 1978). If this is to be a useful measure of productivity, the fall proportion of fawns should reflect the rate at which individuals enter the breeding population in the following spring.

The proportion of fawns in the spring population ( $P_S$ ) is related to the fall proportion of fawns ( $P_f$ ) by the following relationship:

$$\begin{aligned}
 P_S &= f_S / (f_S + d_S) \\
 P_S &= (f_f \cdot S_f) / ([f_f + d_f] \cdot S_t) \\
 P_S &= P_f \cdot S_f / S_t, \qquad (1)
 \end{aligned}$$

where

$f_S$  = the number of fawns in the spring population,  
 $f_f$  = the number of fawns in the fall population,  
 $d_S$  = the number of does in the spring population,  
 $d_f$  = the number of does in the fall population,  
 $S_f$  = the overwinter survival rate of fawns, and  
 $S_t$  = the weighted mean overwinter survival rate of all fawns  
 and does.

The survival rate,  $S_t$ , may be expressed as

$$S_t = S_f \cdot P_f + S_d \cdot (1 - P_f)$$

where

$S_d$  = the survival rate of does over the winter.

If the ratio of survival rates  $S_f$  and  $S_t$  is constant, then the proportion of fawns in the fall population of fawns and does ( $P_f$ ) would be a consistent indicator of the spring proportion ( $P_S$ ) and thus a consistent indicator of productivity as measured by recruitment into the breeding population.

Information collected on survival rates of mule deer suggests that survival rates of fawns and does may differ substantially and are highly variable (Robinette, 1956; Robinette et al., 1957; Robinette, 1977; Zwank, 1978; Medin and Anderson, 1979). This indicates that the ratio of the overwinter survival rate of fawns ( $S_f$ ) and the total overwinter survival rate of fawns and does would not be constant. As a result, the fall proportion of fawns may not be a good indicator of



the productivity of a herd of mule deer as measured by recruitment into the breeding population.

A second measure of productivity that is useful is the rate at which the adult does produce offspring. In this work, it will be referred to as the reproductive performance of a population. The reproductive performances of a single herd from year to year or two or more herds may be compared if information concerning the number of fawns per doe is collected at approximately the same time each year. If does of all age classes produced fawns at similar rates, then the proportion of fawns would provide a comparable measure of productivity between herds.

Reproduction, however, is not evenly spread across age classes. Yearling does of mule deer often produce significantly fewer fawns than do does 2 years of age or older (Robinette and Gashwiler, 1950; Robinette, 1956; Zwank, 1976, 1978; Medin and Anderson, 1979). Thus, as Zwank (1976) points out, "If the previous year's net productivity was high, a large proportion of less productive yearlings are included in the population and fawn:doe ratio. This would tend to depress the apparent size of the present year's fawn crop." Since it is difficult, if not impossible, to distinguish between yearling does and older does (Downing, 1970; Wyoming Game and Fish Dept., 1977; Zwank, 1978), the proportion of fawns among all fawns and does may not be a measure of productivity which allows for meaningful comparisons between herds. This specific problem as well as others discussed here give rise to the main questions being addressed in the research and resulting conclusions reported in the following.

### Definitions

To facilitate clear and unambiguous usage, the following definitions are presented. They are not meant for general acceptance but are intended to provide consistency herein. They are necessary because of the unclear and variable usage in the literature. As far as possible these definitions are those which have been used in other work.

Fawns are deer of both sexes under the age of 1 year.

Does are female deer 1 year of age or older.

Yearlings are deer between one and 2 years of age.

Population is a cluster of individuals with a high probability of mating with each other compared to their probability of mating with a member of some other population (Pianka, 1974). The population of fawns and does refers to the collection of all fawns and does in such a population.

A population of deer is also often referred to as a herd.

Ratio of fawns to does is the number of fawns divided by the number of does (fawns/does).

Proportion of fawns is the number of fawns divided by the total number of fawns and does (fawns/[fawns + does]).

Rate of increase is the rate at which a population increases (or decreases) in numbers over a specified period of time. This rate may be specified as an instantaneous rate or a finite rate over an interval of time. Positive rates of increase mean that a population is growing, while negative rates signify a decline in the size of

a population. A rate of increase of zero means the population is not growing.

Gross productivity is the proportion of the population that could be removed annually on a sustained yield basis if all the young which were conceived were successfully born and survived to the hunting season (Simkin, 1974).

Net productivity is the proportion of a stable population that can be removed on a sustained yield basis after mortality from causes other than hunting have been deducted (Leopold, 1933; Pimlott, 1959; Simkin, 1974).

Recruitment is the addition by reproduction of new individuals to a population (Ricklefs, 1973). In this work it will be expressed quantitatively as the number of fawns per doe which reach 1 year of age.

Reproductive performance of a population is the number of fawns produced per doe 2 years of age or older that are alive at a specified time (this may be at the time of birth, mid-summer, fall, or other time convenient for measurement).

### Objectives

The objectives of this study were to investigate:

- 1) the effect of misclassifying fawns and does on estimates of the proportion of fawns from a sample of fawns and does from a population of mule deer,

- 2) the reliability of using the proportion of fawns in the fall as an index to the rate at which fawns are recruited into population the following spring, and
- 3) the reliability of using the proportion of fawns as an index of the reproductive performance of the population.

These objectives are partially fulfilled through the testing of the following hypotheses.

- H1: Estimates of the proportion of fawns in the fall are not biased by the misclassification of fawns as does and does as fawns.
- H2: There is a high correlation between the proportion of fawns in the fall population and the rate at which individuals are recruited into the spring population.
- H3: The proportion of fawns is highly correlated with the reproductive performance of the population as measured in the fall.

## LITERATURE REVIEW

### Use of Age Ratios

Several relationships between the number of fawns and the number of does have been important in the management of mule deer for many years. In particular, such relationships have been used in determining estimates or indices of productivity as well as other parameters which are used to characterize populations.

The proportion of fawns and the ratio of fawns to does have been widely used in the calculation of measures of the productivity of herds of mule deer (Zwank, 1976). The occurrence of fawns is usually considered to be the best measure of the productivity of a population (Pimlott, 1959). What is specifically meant by productivity, however, is often left uncertain by researchers when using the relationship between the numbers of fawns and does (Caughley, 1974). High ratios of fawns to does frequently is interpreted to mean the population is doing well or at least better than another where ratios are lower (see e.g. Julander et al., 1961; Nellis, 1968; Woodward et al., 1974; Murphy and Whitten, 1976; Wyoming Game and Fish Dept., 1977). Without specifically stating what is meant by productivity, however, these researchers can claim little interpretative power with their analysis.

Despite the nebulous uses of the concept of productivity, at least three parameters which may be said to characterize the productivity of a population have been estimated or indexed using the relationship between the numbers of fawns and does. The first of

these is the rate of recruitment of individuals into the population at a specified time. The rate of recruitment may be estimated at a given time by counting numbers of fawns and does in a binomial sample of a population of deer. The estimate is simply the ratio of individuals counted as fawns to those counted as does. Zwank (1978) used the ratio of fawns to adult does as a measure of recruitment in herds of mule deer in Utah. Kimball and Wolfe (1974) used the ratio of calves to cows to estimate recruitment into herds of elk (Cervus canadensis) in northern Utah.

Estimates of the rate of recruitment using the ratio of fawns to does collected from a binomial sample of the population are subject to major statistical problems. Ratio estimates of this type have an infinite expectation and an undefined variance (Paulik and Robson, 1969; Seber, 1973; Brownie et al., 1978). This makes them difficult to analyze directly from a statistical standpoint, particularly when ratios from different populations or different years are compared. If, however, the relationship between fawns and does is expressed in terms of the proportion of fawns ( $\text{fawns}/[\text{fawns} + \text{does}]$ ) instead of the ratio of fawns to does ( $\text{fawns}/\text{does}$ ), statistical comparisons can be made. The proportion of fawns is statistically a proportion (Freund, 1971). Confidence intervals around estimates of this proportion can be easily calculated according to techniques discussed by Cochran (1963).

Because of the monotonic relationship between the ratio of fawns to does and the proportion of fawns (Figure 1), a confidence interval around estimates of the ratio of fawns to does can be made using techniques outlined by Seber (1973, p. 363-6). Confidence intervals of two ratios calculated by this method can then be compared in testing

for statistical differences. The Wyoming Game and Fish Department (1977) suggests one such confidence interval based on the variance in proportion of fawns.

A second parameter which has been used to characterize the productivity of a herd of mule deer is net productivity. Pimlott (1959) and Simkin (1974) provide two methods that have been used to estimate the net productivity of populations of mule deer utilizing relationships between the numbers of fawns and does just prior to the hunting season. The first method uses the ratio of fawns to does (fawns/does) as an estimate of net productivity. The second method uses the proportion of fawns (fawns/[fawns + does]) as an estimate of net productivity. Estimates for both methods are based on counts of fawns and does in the field.

The proportion of young in the population of young and mature females and the ratio of young to mature females have been used to estimate or as an index of net productivity in several Cervids. Anderson et al. (1970) used the ratio of yearling does to adult does as an index of net productivity in a herd of mule deer in the Guadalupe Mountains, New Mexico. Mansell (1974) used the ratio of fawns to does to estimate net productivity in a herd of white-tailed deer (Odocoileus virginianus) on the Bruce Peninsula, Ontario. Pimlott (1959) and Simkin (1965, 1974) used both the ratio of calves to cows and the proportion of calves as estimates of the net productivity of populations of moose (Alces alces) in Newfoundland and Ontario. Simkin (1974) also lists several other studies where the net productivity of moose were estimated using the ratio of calves to cows or the proportion of calves.

While both methods presented by Simkin and Pimlott appear to be rather simple schemes to estimate net productivity if accurate ratios or proportions can be obtained, neither estimator can be used alone to estimate net productivity. This can be seen quite easily in a simple example. Consider the four populations with fawn production and death rates as shown in Table 1. The ratio of fawns to does in the fall is the same for all populations and similarly the proportion of fawns in each population is the same. Thus, according to these estimators, the net productivity (or proportion of the population which can be harvested to keep the population stable) is the same for each population. However, when the proportion of the population which needs to be harvested to keep the population at the same level (net productivity) is calculated directly from the fall population (see Appendix A), it ranges from 0.00 for population 1 to 0.13 for population 4 if all age classes are harvested at the same rate.

If, for the same populations, only animals of age 2 and older are harvested, the ratio of fawns to does and the proportion of fawns in the population actually decrease as the proportion of the population that can be harvested (net productivity) increases! Numerical examples of this phenomena are shown in Table 2. These examples show quite clearly that the ratio of fawns to does or the proportion of fawns do not represent estimates or even consistent indices of net productivity by themselves. One needs to know both death rates and recruitment rates before net productivity can be calculated (Robinette, 1956).

A third parameter which has been used to characterize the productivity of populations is the rate of increase of the population. The ratio of fawns to does or yearlings to adult does is sometimes



Table 1. Net productivity, ratio of fawns to does, and proportion of fawns in the population for four different populations where all age classes are harvested with equal intensity. (See Appendix A for discussion of model and calculations.)

Population	Fawns Produced Per Doe Surviving to the Fall by Age 1	Per Doe Surviving to Ages 2 to 8	Non-hunting Mortality Rates for all Ages	Pre-hunt Ratio of Fawns to Does	Pre-hunt Fawn Proportion	Net Productivity (Proportion of Population to be Removed)
1	.000	.385	.250	.770	.435	.000
2	.000	.404	.213	.770	.435	.047
3	.000	.423	.175	.770	.435	.091
4	.000	.442	.138	.770	.435	.130

Table 2. Net productivity, ratio of fawns to does, and proportion of fawns in the population for four different populations where only age classes 2 to 8 are harvested. (See Appendix A for discussion of model and calculations.)

Population	Fawns Produced Per Doe Surviving to the Fall by Age 1	Per Doe Surviving to Ages 2 to 8	Non-hunting Mortality Rates for all Ages	Pre-hunt Ratio of Fawns to Does	Pre-hunt Fawn Proportion	Net Productivity (Proportion of Population to be Removed)
1	.000	.385	.250	.770	.435	.000
2	.000	.404	.213	.758	.431	.046
3	.000	.423	.175	.744	.426	.088
4	.000	.442	.138	.731	.422	.125

interpreted as reflecting the rate of increase of a population (Caughley, 1974).

Caughley shows, however, that age ratios cannot be consistently interpreted as an index of the rate of increase of a population without additional demographic information. He presents situations within populations where the age ratios do not consistently reflect changes in the rate of increase of the population. He concludes that "age ratios are not adequate substitutes for accurate estimates of relative or absolute density from which rate of increase can be measured. Nor do they assist in calculation of this rate."

The relationship between the numbers of fawns and does has been used in the estimation or as indicators of other parameters which are used to characterize populations. Paulik and Robson (1969) and Seber (1973) present estimators for the size of the population of fawns and does. These estimators require estimates of the proportion of fawns in the population at two points in time (e.g., pre- and post-hunting season) and an actual count or estimate of the individuals dying during the period between the composition counts. Variance estimates calculated using the delta method (Seber, 1973, p. 7-9) for these estimators are also presented. The numbers of fawns and does in a herd of mule deer near Logan, Utah, are calculated by Seber (1973) using one of these estimators and data collected by D. I. Rasmussen and E. R. Doman.

Hanson (1963) reviews three estimators of absolute rates of mortality which utilize the ratio of fawns to does. Both rates of fawn and doe mortality may be calculated using these estimators. These estimators were developed by D. M. Selleck and C. M. Hart, G. A.

Petrides and W. L. Robinette. While differing slightly in their form, all of these estimators require estimates of the ratio of fawns to does before and after the period of mortality and the ratio of fawns to does among the individuals dying. No estimates of the variance of these estimators are presented, primarily because of the use of ratios instead of proportions (Paulik and Robson, 1969).

Another estimator utilizing the proportion of fawns is an estimate of the ratio of the survival rate of fawns to the survival rate of does (Paulik and Robson, 1969; Seber, 1973). This estimator requires estimates of the proportion of fawns both at the start and at the end of the period of consideration. An estimate of the variance using the delta method is presented in both cases.

The ratio of fawns to does has been used along with birth rates by several researchers as an indicator of the survival rate of fawns during the summer. The number of fawns per doe at a point in time after parturition is compared with the number of fawns produced per doe at parturition. If the mortality rate of the does is near zero during the period of time under consideration, then the difference in the ratio of fawns to does at birth and at the later period indicates the relative rate of survival of fawns; a small difference would suggest high survivorship, a large difference, low survivorship. Nellis (1968) and Smith and LeCount (1979) used this technique to determine the relative survivorship of fawns of mule deer. The relative survivorship of fawns of pronghorn antelope (Antilocapra americana) was determined by Beale and Smith (1978) with this technique. Using a similar approach Wegge (1975) obtained the relative rates of survivorship of calves of Norwegian red deer (Cervus elaphus).

### Errors in Estimates of Fawn Proportions

At least three sources of error or bias in estimating the proportion of fawns have been identified. The first source of error is due to chance from binomial sampling schemes. Leopold (1933) suggested, "as a rule of thumb," that samples of over 100 animals were needed to assure representative estimates. Cochran (1963) and the Wyoming Game and Fish Department (1977) provide methods for the calculation of sample sizes needed to assure estimates within desired levels of accuracy. The accuracy of a given estimate of the proportion of fawns is a non-linear function of the size of the sample and the proportion of fawns (Cochran, 1963).

A second source of error involved in estimating the proportion of fawns may be the result of non-random samples. If each fawn and doe of a population does not have an equal probability of being observed, then the estimated proportion of fawns is generally biased. The non-randomness of the sample may be the result of unequal coverage of areas occupied, in a non-random fashion, by the sampled population. Differential behavior between different age and sex classes can create this type of heterogenous distribution (Hanson, 1963).

The probability of being observed is also affected by visibility which may vary by sex and age. Poux (1972) found that fawns of white-tailed deer were less visible than does until nearly 6 months of age, after which time they were nearly as visible as the does. He also found differences in the visibility of bucks and does during various months of the year. Dasmann and Taber (1956) reported that there were

sexual differences in the visibility of individuals of Columbian black-tailed deer (O. h. columbianus).

A final source of error in estimates of the proportion of fawns may come from the misclassification of individuals (Hanson, 1963). Yearling bucks and fawns may be mistaken for does and does may be mistaken for fawns (Leopold, 1933; Leopold as quoted by Hazzard, 1958; Downing, 1970; Wyoming Game and Fish Dept., 1977). As fawns approach does in body size, the problem of differentiating between them increases greatly (Wyoming Game and Fish Dept., 1977). In a study of white-tailed deer, Downing (1970) found that under nearly ideal conditions of antler development, about five percent of the small antlered bucks were misclassified as does.

## METHODS

Hypothesis H1

The first hypothesis is that the misclassification of does and fawns does not bias estimates of the proportion of fawns. It was tested by comparing the expected value of two random variables (defined below). This method was chosen as it allows for the direct detection of any biases affecting the estimation of the proportion of fawns that would be introduced by the misclassification of fawns and does. Also, the magnitude of any biases could easily be calculated.

The random variables to be compared are estimators of the proportion of fawns ( $P$ ) obtained from a simple random sample of the population with replacement (binomial sampling). The first of these,  $\hat{P}$ , is the estimated proportion of fawns obtained without the misclassification of fawns and does. The other,  $\hat{P}^*$ , is the estimated proportion of fawns obtained with various levels of misclassification of fawns as does and does as fawns. If misclassification does not bias the estimated proportion of fawns in a sample from a population, then the expected value of  $\hat{P}^*$  will equal the expected value of  $\hat{P}$  (Blum and Rosenblatt, 1972). If the expected value of  $\hat{P}^*$  does not equal the expected value of  $\hat{P}$ , then the difference between the two will represent the bias due to misclassification. H1 is to be rejected if  $E(\hat{P}^*)$  is found to be different than  $E(\hat{P})$ .

Throughout the discussion of H1, the following notation will be used.

- $E(r)$  = The expected value of the random variable  $r$ ;
- $f$  = the number of animals counted as fawns in a sample containing  $n$  fawns and does;
- $n$  = the number of fawns and does in a sample;
- $P$  = the proportion of fawns in a population of fawns and does;
- $\hat{P}$  = an unbiased estimate of  $P$ ;
- $P^*$  = the expected value of  $\hat{P}^*$ ;
- $\hat{P}^*$  = an estimate of  $P$  subject to the misclassification of fawns and does;
- $P_{dd}$  = the conditional probability an individual observed is counted as a doe when it is a doe;
- $P_{df}$  = the conditional probability an individual observed is counted as a doe when it is a fawn;
- $P_{fd}$  = the conditional probability of an individual observed is counted as a fawn when it is a doe;
- $P_{ff}$  = the conditional probability an individual observed is counted as a fawn when it is a fawn.

The statistical model which was used as an unbiased estimator of  $P$  when there is no misclassification is

$$\hat{P} = f/n$$

(Paulik and Robson, 1969; Seber, 1973). This estimate would come from the sampling of a population where binomial sampling was used (Seber, 1973), binomial sampling being where each individual has an equal probability of being observed and sampling is done with replacement. This represents the sampling procedure typically used when classifying individuals of deer herds (Wyoming Game and Fish Dept., 1977).

The estimator  $\hat{P}^*$  of  $P$  subject to the misclassification of fawns and does would, like  $\hat{P}$ , be of the form

$$\hat{P}^* = f/n;$$

simply the function of individuals counted as fawns in a sample size  $n$ .

The misclassification of fawns as does was modeled by assuming each fawn had an equal probability of being misclassified as a doe. Thus, if an observer misclassifies 10 percent of the fawns as does, a fawn observed at random would have a probability ( $P_{ff}$ ) equal to 0.9 of being recorded as a fawn and a probability ( $P_{df}$ ) equal to 0.1 of being recorded as a doe. Note that  $P_{ff}$  and  $P_{df}$  will always sum to 1.0. The misclassification of does was also modeled in this manner; each doe was assumed to have an equal probability ( $P_{fd}$ ) of being misclassified as a fawn.

This approach to modeling misclassification was used as it allowed for the case where all fawns or does had essentially equal probabilities of being misclassified. Modifications on this scheme allow for cases where a certain portion of the fawns or does had higher or lower probabilities of being misclassified. This latter situation might arise when fawns with does are less likely to be misclassified than fawns which are observed alone or when yearling does are smaller than adult does and are more likely to be counted as fawns. As long as all individuals have an equal probability of being observed, then the probability of misclassifying a fawn (or doe) may be modeled by using the mean probability of misclassifying a fawn (or doe). This can be seen by calculating the expected value of a random variable representing the probability that an individual observed at random is



misclassified. This expected value is equal to the mean probability of misclassifying an individual.

The estimators  $\hat{P}$  and  $\hat{P}^*$  as developed here assume that  $n$ , the number of fawns and does in a sample, is a fixed value. When the numbers of fawns and does are actually collected, however, the value of  $n$  is generally a random variable with its value dependent upon the sampling effort and chance. Often a minimum value for  $n$  is established for observers, but the total number actually observed is generally still a function of chance.

Assuming  $n$  is fixed instead of a random variable, though, is not a serious problem. Seber (1973) shows that considering  $n$  as fixed or as a random variable produces essentially the same estimates for the expected values and variances for these estimators of  $P$ . Since this is the case, the estimators  $\hat{P}$  and  $\hat{P}^*$  were analyzed with the assumption that  $n$  was fixed before sampling; the expected values and variances of  $\hat{P}$  and  $\hat{P}^*$  are more easily calculated when  $n$  is assumed to be fixed than when it is assumed to be a random variable. The expected values and variances for  $\hat{P}$  and  $\hat{P}^*$  are calculated in Appendix B.

### Hypothesis H2

The second hypothesis is that the proportion of fawns in the fall population is an indicator of the rate of recruitment of fawns into the spring population. It was tested using a model that simulated a population of mule deer in which antlerless individuals are subject to little or no hunting pressure. The model was designed to test H2 on a population of mule deer which is typical of many of the herds in the Intermountain West.

The data needed to test H2 were an exact knowledge of the rate of recruitment of fawns into the spring population and the proportion of fawns in the population in the previous fall for many different years. The best data to provide the most realistic analysis would come from field studies. Such data, however, do not exist from field studies even from extensively studied herds such as the herd of white-tailed deer on the George Reserve in Michigan (O'Roke and Hamerstrom, 1948; McCullough, 1979). Because of this lack of necessary data from field studies, a model that simulates the dynamics observed in a real population was developed and used to simulate a deer population (typical of the Intermountain West) over a period of years. Exact rates of recruitment into the spring population by fawns and the proportion of fawns in the fall population were then calculated from the simulated population.

A variable projection matrix model (Fowler and Smith, 1973; Smith, 1973) was used to generate the data required for testing H2. This model, a modification of the classical Leslie matrix model (Leslie, 1945, 1948) was selected as it allows for the examination of the dynamics of separate age classes and because it produces more realistic dynamics than possible in simpler models.

Two projection matrices were used for simulation over time. One matrix was used to predict the spring population of deer (late May) from the preceeding fall (late October) while the other matrix was used to predict the fall population from the previous spring. Only the female portion of the non-fawn population and all of the fawns to an age of 1 year were considered in the testing of H2.

Shown in Figure 2 is the projection matrix (A) used to predict the spring population from the preceding fall. This matrix is multiplied by a vector ( $N_f$ ) representing the age structure in the fall population to produce a vector ( $N_s$ ) representing the age structure in the spring population. The multiplication of  $N_f$  by matrix A advances each age class one year (age class  $i$  becomes age class  $i + 1$ ) and calculates the number of fawns at the time of parturition. The subdiagonal elements ( $s_i$ ) of matrix A are the survival rates of does in age class  $i$  from fall to spring. The top row of elements ( $b_i$ ) contains the average number of fawns produced by a doe of age class  $i$  that are alive to bear young in the spring. As shown by Fowler and Ryel (1979),

$$b_i = f_i \cdot s_i$$

where

$f_i$  = the average number of fawns produced by a doe from age class  $i$  ( $i$  being the age class in the fall) which are alive in the spring.

The matrix B used to calculate the fall population from the spring population is shown in Figure 3. A vector ( $N_s$ ) representing the population in the spring is multiplied by matrix B to produce a vector ( $N_f$ ) representing the fall population. The non-zero elements of matrix B consist of a set of survival rates on the diagonal. These survival rates ( $s'_i$ ) represent the proportion of individuals in age class  $i$  surviving from spring to fall.

An important aspect of survival and fecundity rates of animal populations is that they usually vary from year to year in response to food availability and winter severity among other factors (Anderson et al., 1974). In this model, the variability in these rates was

$$\begin{bmatrix}
 b_1 & b_2 & \cdots & b_m \\
 s_1 & 0 & \cdots & 0 \\
 0 & s_2 & & \cdot \\
 \vdots & & \ddots & \cdot \\
 0 & \cdots & s_{m-1} & 0
 \end{bmatrix}
 \begin{bmatrix}
 n_{1,f} \\
 n_{2,f} \\
 \cdot \\
 \cdot \\
 n_{m,f}
 \end{bmatrix}
 =
 \begin{bmatrix}
 n_{1,s} \\
 n_{2,s} \\
 \cdot \\
 \cdot \\
 n_{m,s}
 \end{bmatrix}$$

A
 $N_f$ 
 $N_s$

Figure 2. Projection matrix (A) used to predict the spring population ( $N_s$ ) from the fall population ( $N_f$ ).

$$\begin{bmatrix}
 s_1' & 0 & \cdots & 0 \\
 0 & s_2' & \cdots & 0 \\
 \cdot & & \ddots & \cdot \\
 \cdot & & & \cdot \\
 0 & \cdot & \cdot & s_m'
 \end{bmatrix}
 \begin{bmatrix}
 n_{1,s} \\
 n_{2,s} \\
 \cdot \\
 \cdot \\
 n_{m,s}
 \end{bmatrix}
 =
 \begin{bmatrix}
 n_{1,f} \\
 n_{2,f} \\
 \cdot \\
 \cdot \\
 n_{m,f}
 \end{bmatrix}$$

B
 $N_s$ 
 $N_f$

Figure 3. Projection matrix (B) used to predict the fall population ( $N_f$ ) from the spring population ( $N_s$ ).

modeled by randomly selecting the rates from sets of realistic values each time the matrices A or B were used.

The set of values used for each rate was determined from studies reported in the literature concerning mule deer (see later). Minimum and maximum values for each parameter were obtained from these studies and a median value determined. Each time matrices A and B were used, uniformly distributed random numbers between -1 and 1 were generated. These random numbers were then multiplied by specific modifying factors and then added to the median values of each rate. The modifier values were such that when multiplied by 1 (or -1) and added to the median value, the maximum (or minimum) value of each rate was produced. This procedure produced a set of values uniformly distributed between the minimum and maximum values for each rate.

Since conditions which are favorable or unfavorable to reproduction and survivorship might be expected to affect all age classes, the rates within each set of fecundity and survival rates were assumed to be highly correlated. When matrix A was used to predict spring population values, two random numbers were generated. One was used to generate the  $f_i$  values while the other was used to select the  $s_j$  rates for a given year. When B was used, one random number was generated; it was used to generate the  $s'_j$  values for a given year. A complete list of assumptions for this model of a population of mule deer appears in Table 3.

The minimum and maximum values for the age specific rates of fecundity and survival used in this model are listed in Table 4. Listed in Table 5 are the ranges of rates of fecundity found for mule deer in

Table 3. List of important assumptions included in the model of a population of mule deer.

- 
- 
1. a. There is a high correlation ( $r \approx 1.0$ ) between the age specific rates of fecundity in a given year.  
b. There is no correlation ( $r \approx 0.0$ ) between the rates of fecundity between years.
  2. a. There is a high correlation ( $r \approx 1.0$ ) between the age specific rates of summer survival in a given year.  
b. There is no correlation ( $r \approx 0.0$ ) between the rates of summer survival between years.
  3. a. There is a high correlation ( $r \approx 1.0$ ) between the age specific rates of winter survival in a given year.  
b. There is no correlation ( $r \approx 0.0$ ) between the rates of winter survival between years.
  4. There is no correlation ( $r \approx 0.0$ ) between the rates of fecundity, winter survival and summer survival.
  5. Rates of fecundity and survival are approximately uniformly distributed between high and low values.
-

Table 4. The minimum and maximum age-specific rates of fecundity ( $f_i$ ), winter survival ( $s_i$ ), and summer survival ( $s'_i$ ).<sup>a</sup>

Age class (i)	$f_i$		$s'_i$		$s_i$	
	Min.	Max.	Min.	Max.	Min.	Max.
1	.000	.026	.550	.890	.400	.870
2	.720	1.230	.860	.960	.680	.900
3+	1.290	1.930	.860	.960	.807	.907

<sup>a</sup>Sources of data found in text.

Table 5. Numbers of fawns produced per doe of age i in the spring.

1	Age i		Source
	2	3+	
.000	.78	1.63	Robinette and Gashwiler (1950)
		1.29	Robinette et al. (1955)
	.75		Trainer and Van Dyke (1975)
	.72		Papez (1976)
.026	1.23	1.93	Zwank (1978)
.000	1.01	1.58	Medin and Anderson (1979)

six studies. The minimum and maximum values reported in these studies were used as the minimum and maximum values in the model.

Summer rates of survival ( $s'_i$ ) were obtained from several sources. Rates of survival of 0.550 and 0.890 for fawns for the first 5 months of life (May to October) have been reported by Robinette et al. (1977) and Zwank (1978). This was the range used in the model for  $s'_i$ .

Medin and Anderson (1979) calculated annual rates of survival of adult does of 0.80 in their work. Distributed evenly throughout the year, this implies a survival rate of 0.910 over the period from late May to late October. This was used as a mean summer survival rate of ages 2 and older. A range of 0.860 and 0.960 was used for these survival rates. The upper level of 0.960 agrees with values found by Robinette et al. (1977).

Overwinter (late October to late May) rates of survival also came from several sources. Robinette et al. (1977) reported an overwinter rate of survival for fawns of 0.870. This was used as a maximum value. Robinette et al. (1957) found that rates of fawn mortality were 2.5 to 3 times that of adults. This was used in conjunction with adult rates to obtain a low value.

Yearling mortality rates over the winter were reported to range from being the same as adults (Robinette et al., 1977; Zwank, 1978) to 1.6 times that of adults (Robinette et al., 1957). The upper rate of survival for yearlings ( $s_2$ ) was assumed to be the same as adults, while the lower values were determined such that the mortality rate for yearlings was 1.6 times that of adults.

The overwinter rates of survival for adults, using the work of Medin and Anderson (1979), would be 0.880. This value, however, when



used with the median values for the other rates of survival and fecundity produces a population which increases slowly. A value of 0.857 creates a stable population in combination with the median values for each parameter and was chosen as the median. A range of 0.807 to 0.907 was then used for the range of rates of overwinter survival of adults. This made the range of rates of overwinter survival of fawns and yearlings become 0.400 to 0.870 and 0.680 to 0.900, respectively.

Twelve age classes of does were considered in this matrix model. Individuals that reached older ages were not considered (they were assumed to die at 12 years) as their total numerical contribution to the population of does was less than 3 percent. The truncation of the population at 12 age classes made this model similar to that of other models of mule deer (Anderson et al., 1974; Medin and Anderson, 1979).

This model was coded into FORTRAN IV (as described in Burroughs Corp., 1978) for high speed simulation on the Burrough's 6700 computer at Utah State University. A listing of the FORTRAN code of the model, a description of parameters and important variables contained in the model, and model validation and verification appear in Appendix C.

Hypothesis H2 was tested using this model to simulate a population of mule deer over a period of 1050 years. Each simulation was begun with the population in a stable age structure as determined by the rate of increase of the population when the median value for each rate of fecundity and survival were used. The first 50 years were discarded from the analysis of the population to remove any effects of the initial stable age distribution. The proportion of fawns in the fall population, the rate of recruitment of fawns into the spring population

(fawns per doe) and the rate of increase of the population were calculated for each of the remaining 1000 years.

The coefficient of linear correlation ( $r$ ) was used to express the strength of the relationship between the proportion of fawns in the fall population and the number of fawns per doe which were recruited into the spring population. An important assumption concerning the calculated coefficient of linear correlation is that the independent variable, in this case the fall proportion of fawns, must be independent (Ott, 1977). Since the age structure of the population in one fall is derived from the previous fall, one might expect that the fall proportion of fawns determined by the age structure of the population each year might be serially correlated and, as a result, not be independent.

To test for serial correlation between the proportion of fawns in the population calculated for the fall each year, the serial correlations between the proportion of fawns in the fall of year  $i$  and the proportions in the fall of years  $i + 1$ ,  $i + 2$ ,  $i + 3$ ,  $i + 4$ , and  $i + 5$  were calculated for several 1000-year simulations of the model as described by Burington and May (1970). The correlation between the proportions in years  $i$  and  $i + 1$  were found to be significantly different than zero ( $P < 0.05$ ) while the correlations between year  $i$  and year  $i + j$  where  $j$  is greater than 1 were found to be insignificant ( $P > 0.05$ ). The correlations between the proportions in years  $i$  and  $i + 1$  were relatively small, being in the range of -0.26 to -0.20; the other correlations were less than 0.05.

To insure the independence between the fall proportions of fawns used in calculating the coefficients of correlation for testing  $H_2$ ,

only 200 out of the 1000 pairs of fall proportions of fawns and spring rates of recruitment calculated in a 1000-year simulation were used. One year out of each 5-year interval of the simulation was randomly selected to produce the 200 years of proportions and rates of recruitments to be considered. The selection process was designed such that two consecutive years could not be chosen.

Five simulations of populations of mule deer over a period of 1050 years (in which the last 1000 years were considered) using different sequences of random numbers were made to test H2. Coefficients of linear correlation between the proportion of fawns in the fall population and the number of fawns per doe that were recruited into the population the following spring were calculated for each of the five simulations for 200 randomly selected years. A coefficient of linear correlation ( $r$ ) for this relationship significantly less than 0.90 was set as the criterion for rejection of H2. The sign test (Ott, 1977) was used to determine if these correlation coefficients were significantly less ( $P < 0.05$ ) than 0.90. Rejection would mean that less than 81 percent ( $r^2$ ) of the variability (Ott, 1977) in the recruitment rate may be accounted for by the proportion of fawns in the population in the previous fall.

### Hypothesis H3

The third hypothesis is that the proportion of fawns in the population is an indicator of the reproductive performance of a population. This hypothesis was tested using the same model developed to test H2.

The reproductive performance of a population was defined earlier to be the number of fawns produced per doe 2 or more years of age that

are alive at a specified time. Since composition counts are frequently taken in the fall, the reproductive performance was measured for the population in late October. The proportion of fawns in the population in October was correlated with the number of fawns surviving to October produced per doe 2 or more years of age to test H3.

To test H3, ten 1050-year simulations were made using the model. The first 50 years of each simulation were discarded and 200 years out of the remaining 1000 were randomly selected to be used in testing H3. The ranges of rates of fecundity and survivorship were the same as used in testing H2. The coefficient of linear correlation between the proportion of fawns among all fawns and does in October and the number of fawns surviving to October produced per doe aged 2 years or older was calculated for the 200 randomly selected years for each of the ten simulations. A coefficient of correlation between these quantities significantly less than 0.90 ( $P < 0.05$ ) would result in rejection of H3. The sign test was used to test whether or not these correlation coefficients were significantly less than 0.90.

## RESULTS AND DISCUSSION

Misclassification

The effect of misclassifying fawns as does and does as fawns on estimates of the proportion of fawns was investigated by the comparison of the expected value of two random variables,  $\hat{P}$  and  $\hat{P}^*$ . As defined earlier, these random variables are estimates of the proportion ( $P$ ) of fawns among does and fawns in a herd of deer.  $\hat{P}$  is an estimate without the misclassification of individuals while  $\hat{P}^*$  is an estimate with the misclassification of fawns and does at specified levels.

If the misclassification of fawns as does and does as fawns does not bias estimates of  $P$ , then the expected value of  $\hat{P}^*$  ( $E[\hat{P}^*]$ ) will equal the expected value of  $\hat{P}$  ( $E[\hat{P}]$ ). As discussed in Appendix B,

$$E(\hat{P}) = P \quad (2)$$

and  $E(\hat{P}^*) = P \cdot P_{ff} + (1-P) \cdot P_{fd}$ . (3)

Thus, if  $\hat{P}^*$  is an unbiased estimate of  $P$ , then

$$E(\hat{P}) = E(\hat{P}^*) \text{ or}$$

$$P = P \cdot P_{ff} + (1-P) \cdot P_{fd}.$$

This implies that  $E(\hat{P}) = E(\hat{P}^*)$  when either

$$P_{df} = 0 \text{ and } P_{fd} = 0 \quad (\text{case I})$$

or  $P_{fd}/P_{df} = P/(1-P)$  (case II)

where

$$P_{df} = 1 - P_{ff}.$$

Case I is simply the situation where no misclassification occurs and as is expected, the estimate of the proportion of fawns ( $P$ ) is unbiased.

Case II is a special situation where the ratio of the probabilities of misclassifying does as fawns ( $P_{fd}$ ) and misclassifying fawns as does ( $P_{df}$ ) happens to equal the actual ratio of fawns to does in the population. Thus, except in the special situation described in case II, misclassification of fawns and does will produce biased estimates of the proportion of fawns ( $P$ ) among fawns and does in a given population.

These findings do not support the hypothesis (H1) that the misclassification of fawns and does will not bias estimates of the proportion of fawns. Misclassification, in general, will bias estimates of this proportion. Thus, H1 must be rejected.

Because the misclassification of fawns and does produces biased estimates of the proportion of fawns, some of the properties of this bias were evaluated. The amount of bias in estimates of  $P$  produced by given levels of misclassification of fawns and does can be expressed by taking the difference between the expected value of  $\hat{P}^*$  ( $E[\hat{P}^*]$ ) and the expected value of  $\hat{P}$  ( $E[\hat{P}]$ ). In other words,

$$\begin{aligned} \text{Bias} &= E(\hat{P}^*) - E(\hat{P}) \\ &= P \cdot P_{ff} + (1-P) \cdot P_{fd} - P \\ &= P_{fd} - P(P_{fd} + P_{df}) \end{aligned} \quad (4)$$

where  $P_{df} = 1 - P_{ff}$ .

This implies that the amount of bias and whether the bias is positive or negative are functions of the probabilities of misclassifying fawns and does ( $P_{fd}$  and  $P_{df}$ ) and the proportion of fawns. The biases produced for a few probabilities of misclassification as a function of the actual proportion of fawns are illustrated in Figure 4.

Two important points can be made about the biases in estimates of the proportion of fawns due to the misclassification of fawns. First,

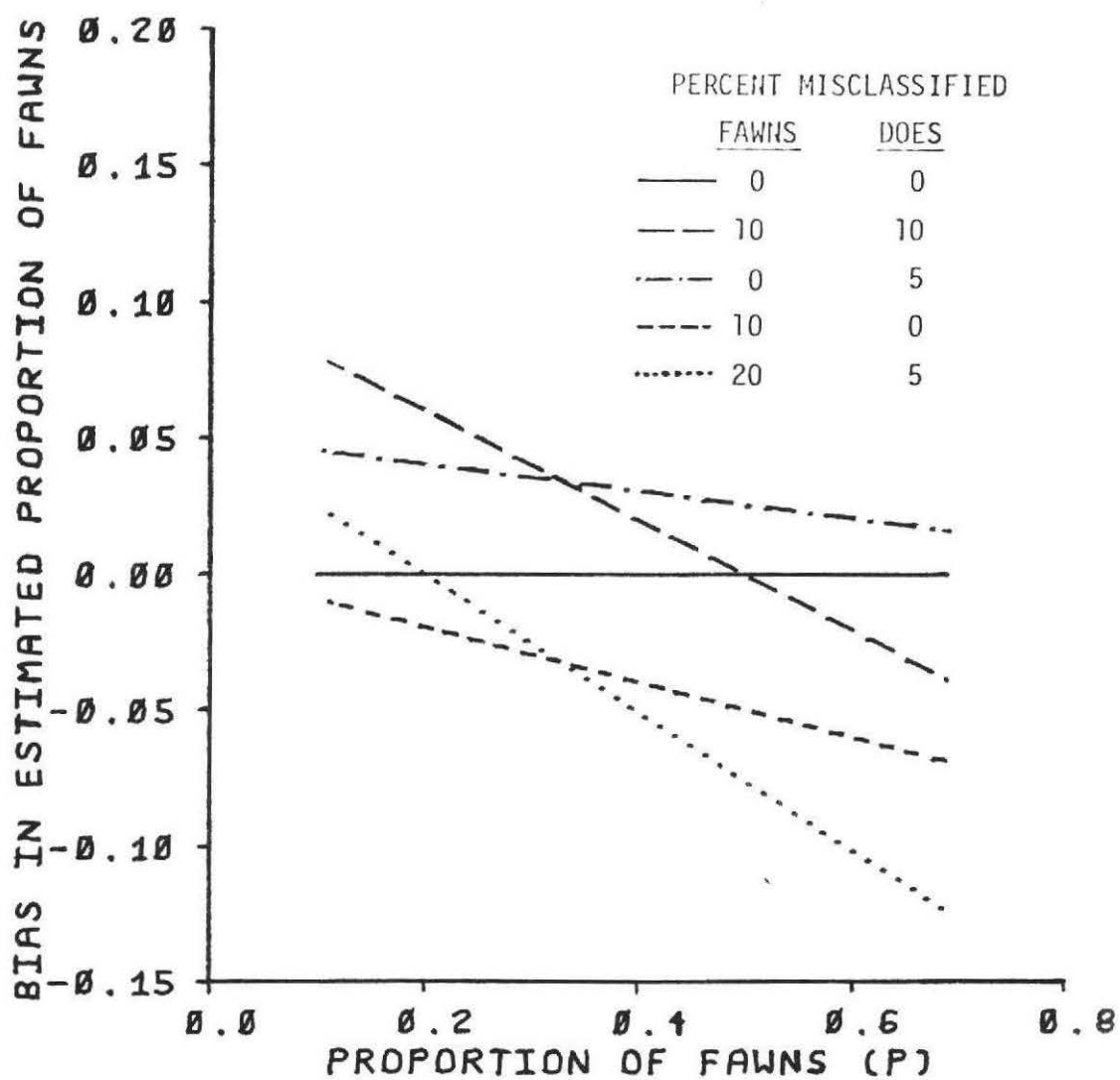


Figure 4. Biases in estimated proportion of fawns in the population of fawns and does with various levels of fawn and does misclassification.

for constant probabilities of misclassifying fawns and does, the amount of bias is different for different proportions of fawns. As can be seen in Figure 4, the bias for given probabilities of misclassifying fawns as does ( $P_{fd}$ ) and does as fawns ( $P_{df}$ ) may be positive, negative or even zero depending on the proportion of fawns.

Second, different probabilities of misclassification produce different amounts of bias in the estimate of the proportion of fawns in a given population. The bias in the estimate of this proportion for a given population produced by misclassification, may be positive, negative or zero depending on the probabilities of misclassifying fawns as does ( $P_{fd}$ ) and does as fawns ( $P_{df}$ ). This also can be seen in Figure 4. Thus, one would have to have a relatively accurate estimate of the probabilities of misclassification ( $P_{df}$  and  $P_{fd}$ ) before much could be said about the amount of bias in the estimate of the proportion of fawns produced by misclassifying fawns and does. If only fawns are misclassified ( $P_{df} \neq 0$ ,  $P_{fd} = 0$ ), however, the bias would always be negative while if only does are misclassified ( $P_{fd} \neq 0$ ,  $P_{df} = 0$ ), the bias would be positive (see equation 4).

While the misclassification of fawns and does biases estimates of the proportion of fawns, it is important to look at the magnitude of the bias in terms of the actual value of this proportion and the effect of the bias on the sampling distribution. If the bias is small relative to the value of this proportion, then it may be considered insignificant. If, on the other hand, the bias is large, then misclassification may cause relatively poor estimates of the proportion of fawns and may lead to false interpretations about the proportion of fawns in a given population.



The relative size and importance of the bias was investigated two ways. First, the percentage increase or decrease in the estimate of the proportion of fawns as a result of the bias was calculated. This percentage was calculated by dividing the bias by the proportion of fawns,  $P$ , and multiplying this quotient by 100. In other words, if PID is the percent increase or decrease in the expected value of estimates of the proportion of fawns due to misclassification, then

$$\begin{aligned} \text{PID} &= \text{Bias}/P \times 100 \\ &= (P_{fd} - P \cdot [P_{fd} + P_{df}])/P \times 100 \\ &= (P_{fd}/P - [P_{fd} + P_{df}]) \times 100. \end{aligned} \quad (5)$$

Values of PID as a function of the proportion of fawns ( $P$ ) are illustrated in Figure 5 for various probabilities of misclassifying does and fawns ( $P_{fd}$  and  $P_{df}$ ).

From this analysis of the magnitude of the bias due to misclassification, two points may be made. First, the bias may be quite large. In one case illustrated in Figure 5, the bias was equal to 80 percent of the value of the proportion of fawns ( $P$ ), an amount which would increase the expected value of estimates of the proportion of fawns to 1.8 times that of the proportion,  $P$ . Second, the type of misclassification is important in determining the magnitude of the bias. If only fawns are misclassified, then the bias simply decreases estimates of the proportion of fawns by an amount equal to the probability of misclassifying fawns as does,  $P_{df}$ . If only does, or both does and fawns are misclassified, the magnitude of the bias may vary greatly with the proportion of fawns,  $P$ .

In the examples presented in Figure 5, the magnitude of the percent increase or decrease (PID) was greatest when the proportion of

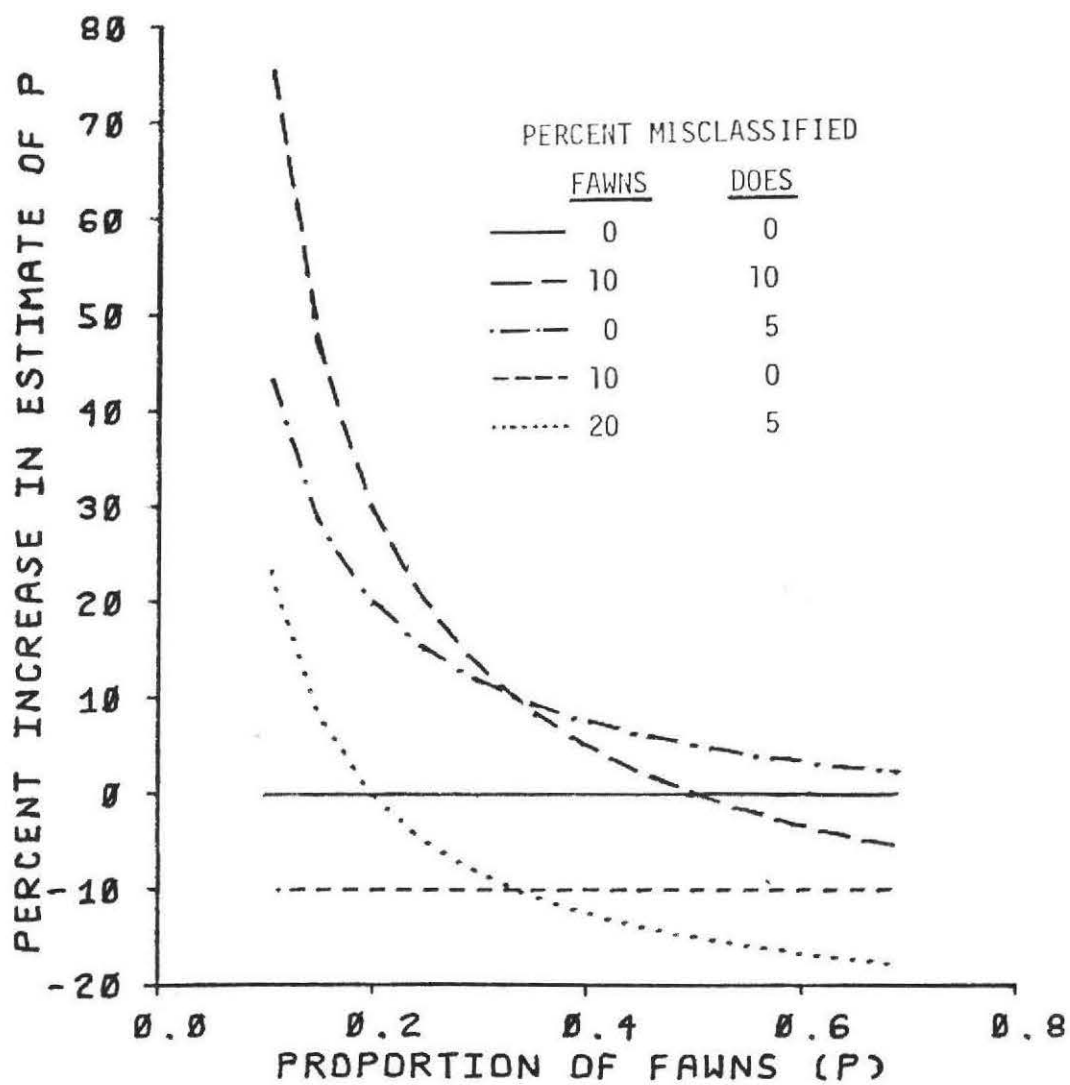


Figure 5. Percent changes in value of the proportion of fawns (P) due to misclassification at various levels.

fawns was small, particularly below 0.25. This would be expected in general as the misclassification of some of the proportionally large number of does would add a relatively large number of "fawns" to the total number of fawns in a sample. As was the case with the actual value of the bias, however, the magnitude of the bias relative to the proportion of fawns,  $P$ , varies greatly with the value of this proportion and the probabilities of misclassification,  $P_{fd}$  and  $P_{df}$ .

The second scheme used to investigate the relative size and importance of the bias due to misclassification involved the investigation of the sampling distributions of the estimators of the proportion of fawns ( $P$ ). The sampling distribution of an estimator of the proportion of fawns describes the probability that when a sample of fawns and does is taken, the resulting estimate of this proportion will be a specific value. The majority of these estimates will be within a specific range of values as determined by their probabilities of occurrence.

If the estimates of the proportion of fawns are biased by misclassification, then the sampling distribution which describes their probabilities of occurrence will be different than the sampling distribution for an unbiased estimator. As a result, the majority of biased estimates will be within a range of values that is different than that of unbiased estimates. Because of this difference in sampling distributions, the bias due to misclassification may cause the range of the majority of the biased estimates to not include the proportion of fawns,  $P$ . If this were the case, the probability that an estimate of the proportion of fawns would be close to that of the proportion,  $P$ , would be very unlikely.

This investigation was undertaken by determining the range of values which includes approximately 95 percent of the biased estimates,  $\hat{P}^*$ , of the proportion of fawns,  $P$  (the bias being the result of misclassification). This range of values was then examined to see whether it included the proportion of fawns,  $P$ . As calculated in Appendix B, the variance of the estimator,  $\hat{P}^*$ , is

$$V(\hat{P}^*) = P^* \cdot (1-P)/n \quad (6)$$

where

$$P^* = E(\hat{P}^*) = P \cdot P_{ff} + (1-P) \cdot P_{fd}.$$

Since proportions are approximately normally distributed in most instances (Blum and Rosenblatt, 1971 and Ott, 1977), the range of values (centered around  $P^*$ ) which includes approximately 95 percent of the estimates obtained from samples containing  $n$  fawns and does would be

$$P^* \pm 1.96 \sqrt{P^* \cdot (1-P^*)/n}. \quad (7)$$

Thus, the range of 95 percent of the estimates includes the actual fawn proportion,  $P$ , when

$$|P^* - P| < 1.96 \sqrt{P^* \cdot (1-P^*)/n} \quad (8)$$

where  $|P^* - P|$  is the absolute value of the difference between  $P^*$  and  $P$ .

Any time the conditions in the inequality (8) are not met, the range of values within which 95 percent of the estimates would fall does not include the proportion of fawns,  $P$ . Figure 6 illustrates an example where 95 percent of the sampling distribution contains the value of  $P$  for most sample sizes while Figure 7 illustrates an example where this is the case only when sample sizes are less than 92 fawns and does.

The significance of the relationship expressed in equation 7 is twofold. First, if the expected value of the biased estimate,  $\hat{P}^*$ , and the proportion of fawns,  $P$ , differ by 0.1 or more (i.e., the bias due to

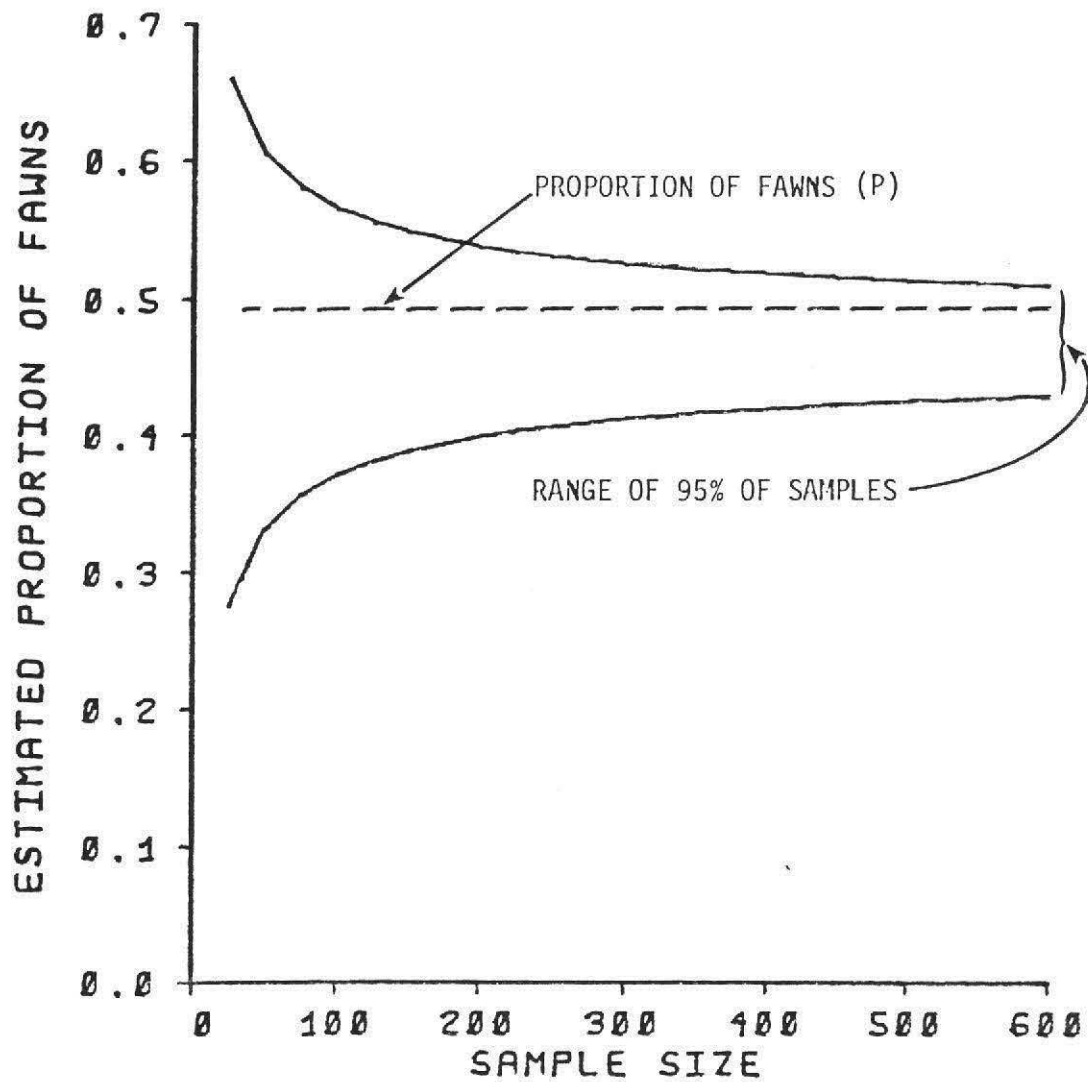


Figure 6. The range which includes 95% of the estimates of the proportion of fawns (P) for various sample sizes of fawns and does where 10% of the fawns are misclassified but none of the does are misclassified.

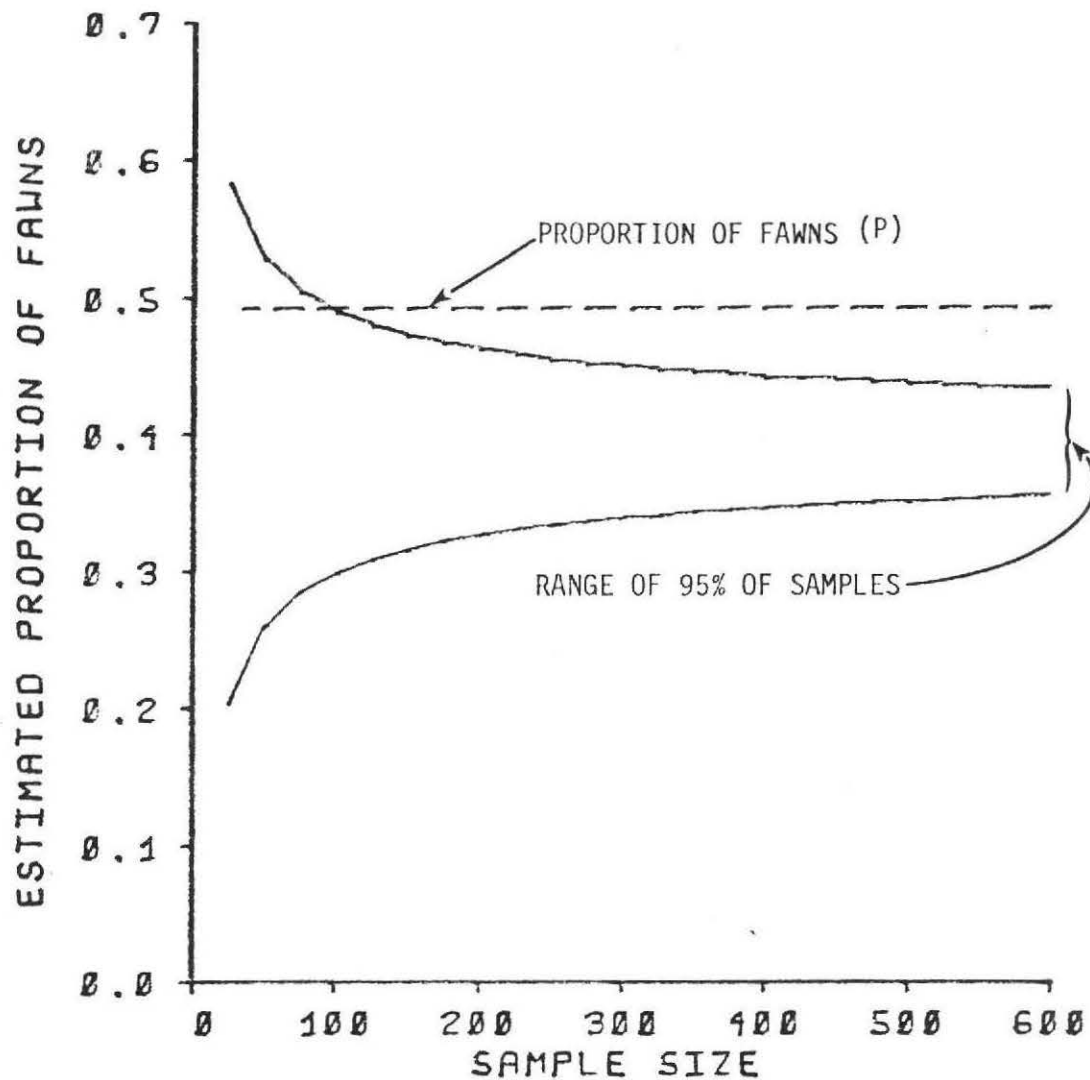


Figure 7. The range which includes 95% of the estimates of the proportion of fawns (P) for various sample sizes of fawns and does where 20% of the fawns are misclassified but none of the does are misclassified.

misclassification is 0.1 or more), then the range of values within which 95 percent of the biased estimates ( $\hat{P}^*$ ) fall will not contain  $P$  for samples of over 100 fawns and does. Thus, if misclassification causes biases of 0.1 or more, an estimate near the value of the proportion of fawns,  $P$ , would be quite unlikely for sample sizes often collected.

The second significant result of (8) is that increasing the size of the sample of fawns and does,  $n$ , will not improve the quality by removing the bias) of the estimate of the proportion of fawns when there is misclassification of fawns and does. As can be seen in equation 6, the range of values within which 95 percent of the biased estimates,  $\hat{P}^*$ , would fall decreases as the sample size,  $n$ , increases. However, as the sample size increases, the estimates of the proportion of fawns,  $P$ , would tend to fall closer and closer to the expected value of the biased estimates,  $P^*$ , not the desired proportion,  $P$ . Thus, while larger sample sizes will decrease sampling errors (by decreasing the variance), they will not produce better estimates of the proportion of fawns,  $P$ , (by removing the bias) as long as misclassification occurs. The bias due to misclassification is unaffected by the size of the sample of fawns and does,  $n$ .

Since the misclassification of fawns and does produces biased estimates of the proportion of fawns ( $P$ ), one might expect that misclassification would also bias other estimators which utilize estimates of  $P$ . As a tangent to the main issues being addressed in this thesis, the effect of misclassification of fawns and does was superficially investigated for a change-in-ratio estimator for population size outlined by Paulik and Robson (1969). This estimator for the population size of fawns and does at time  $t_1$  may be expressed as:

$$\hat{N}_{t1} = (R_f - R \cdot \hat{P}_{t2}) / (\hat{P}_{t1} - \hat{P}_{t2}) \quad (9)$$

where

$\hat{N}_{t1}$  = the estimated number of fawns and does in a population at time  $t1$ ;

$\hat{P}_{ti}$  = an estimate of the proportion of fawns in the population at time  $i$ ;

$R_f$  = the number of fawns removed from the population between times  $t1$  and  $t2$  (must be known exactly); and

$R$  = the number of fawns and does removed from the population between times  $t1$  and  $t2$  (must be known exactly).

Table 6 shows values of  $\hat{N}_{t1}$  calculated using  $P$  and  $P^*$  for a few values of misclassification,  $P_{fd}$  and  $P_{df}$ , where the probabilities of misclassification were assumed to be the same at times  $t1$  and  $t2$ . The differences in the values of  $\hat{N}_{t1}$  calculated using  $P$  and  $P^*$  suggest that misclassification of fawns and does will cause biases in the estimator  $\hat{N}_{t1}$ . The statistical properties of this problem need further study.

#### Fall Proportion of Fawns as Index of Spring Recruitment

The use of the proportion of fawns in the fall population as an index of spring recruitment rates was investigated using the model for simulating mule deer populations as described in the methods section. The coefficients of linear correlation ( $r$ ) between the fall proportion of fawns and the number of fawns per doe recruited into the population the following spring for five simulations of 1000 years each are shown in Table 7. These represent correlations between these parameters calculated for 200 randomly selected years from each of the 1000-year simulations.



Table 6. Estimates of  $N_{t1}$  for a hypothetical population using P and P\* for four sets of probabilities of misclassification ( $P_{df}$  and  $P_{fd}$ ).

Parameter values	$P_{df} = .10$ $P_{fd} = .10$	$P_{df} = .00$ $P_{fd} = .05$	$P_{df} = .10$ $P_{fd} = .00$	$P_{df} = .20$ $P_{fd} = .05$
Actual $N_{t1}$	10000	10000	10000	10000
No. of fawns at $t_1$	4000	4000	4000	4000
No. of does at $t_1$	6000	6000	6000	6000
$R_f$	30	30	30	30
$R$	230	230	230	230
$P_{t1}$	.4000	.4000	.4000	.4000
$P_{t2}$	.4063	.4063	.4063	.4063
$P_{t1}^*$	.4200	.4300	.3600	.3500
$P_{t2}^*$	.4251	.4360	.3657	.3548
$\hat{N}_{t1}$ using P	10000	10000	10000	10000
$\hat{N}_{t1}$ using P*	13349	11659	9475	10840

Table 7. Correlation coefficient between the proportion of fawns in the fall and the rate of recruitment in the following spring.

Simulation run	Coefficient of correlation
1	.878
2	.829
3	.872
4	.835
5	.867
-----	
$\bar{x}$	.856
$S_{\bar{x}}$	.010
95% C.I.	(.828, .884)

The coefficients of correlation calculated from the five simulations ranged from 0.829 to 0.878 with a mean of 0.856. If these estimates of the correlation are approximately normally distributed, the 95 percent confidence interval for the coefficient of correlation ( $r$ ) would be (0.828, 0.884). Thus, as an index, the fall proportion of fawns can explain only about 73 percent ( $r^2$ ) of the variability in the rate of recruitment in the following spring for populations similar to the model constructed. A scattergram showing a sampling of the fall proportion of fawns and the spring recruitment rates appears in Figure 8 for the first of the series of five simulations.

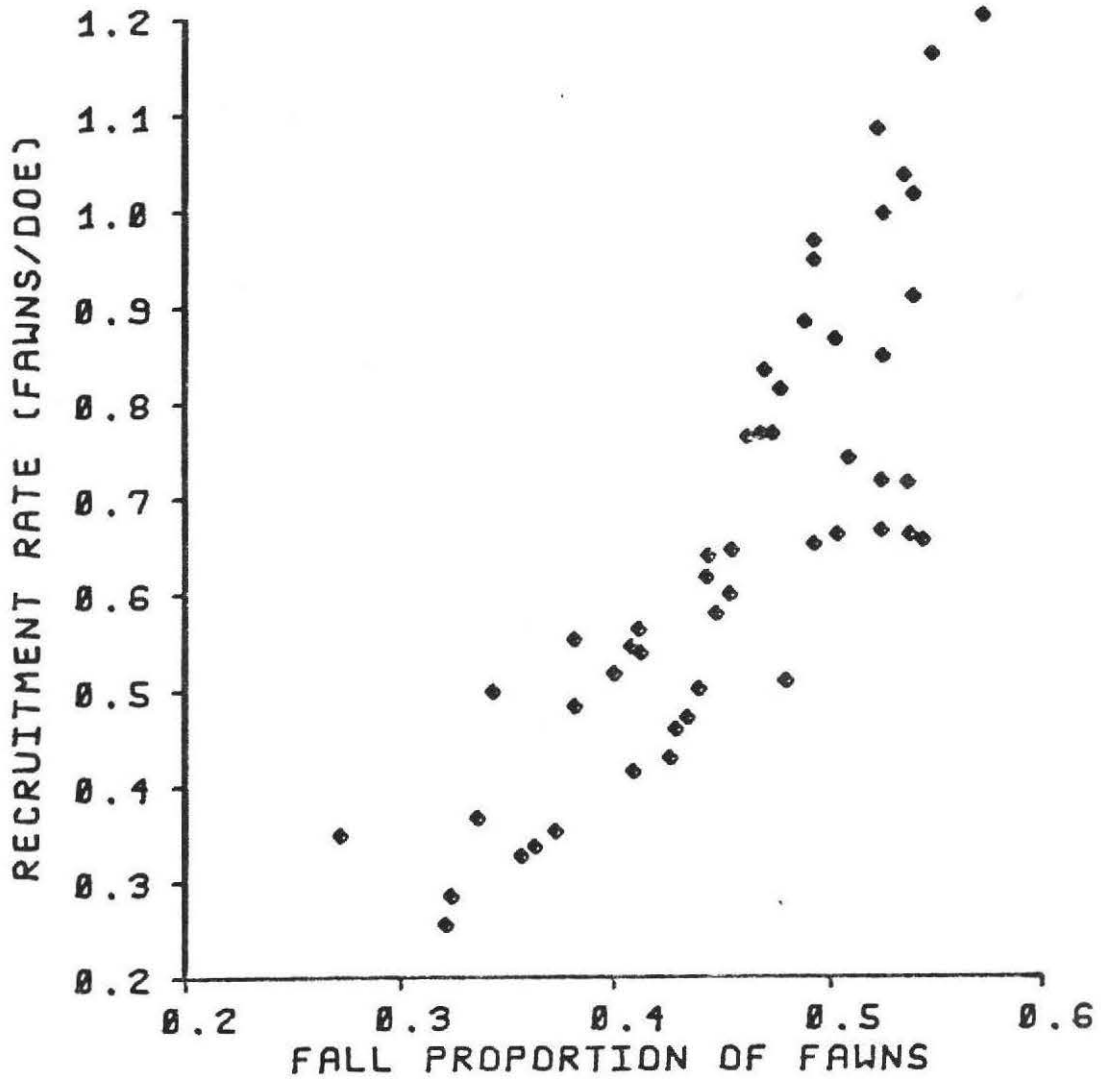


Figure 8. Scattergram showing relationship between fall proportion of fawns and rate of recruitment in following spring.

The correlation between the fall proportion of fawns and the rate of recruitment of fawns into the population the following spring discussed here was determined under conditions wherein the exact fall proportion of fawns was known from the simulated population. However, only estimates of this quantity are generally known for free ranging wild populations, having been gathered from samples of various sizes through binomial sampling. Since sampling adds variability to the calculated fall proportions, one might expect the correlations between the fall proportions and rates of spring recruitment to vary with the accuracy of these estimates, the smaller the sample size, the smaller the correlation.

The coefficients of correlation ( $r$ ) between estimates of the fall proportion of fawns and the rate of recruitment of fawns (fawns per doe) into the population the following spring were calculated for sample sizes of 50, 100, 200, and 500 fawns and does. The number of fawns and does contained in a sample of a given size were randomly selected from binomial distributions each fall in the simulations. The correlations calculated for each sized sample are shown in Figure 9. Five simulations were made for each sample size; the 95 percent confidence intervals for each coefficient of correlation calculated from the five simulations are shown. The mean correlation coefficients calculated for the cases where the fall proportion of fawns were estimated from samples of 50, 100, 200, and 500 fawns and does were 0.604, 0.719, 0.767, and 0.824, respectively. The coefficient of correlation when fall proportions of fawns are known (approximately 0.856) is an asymptote as the sample size becomes large.

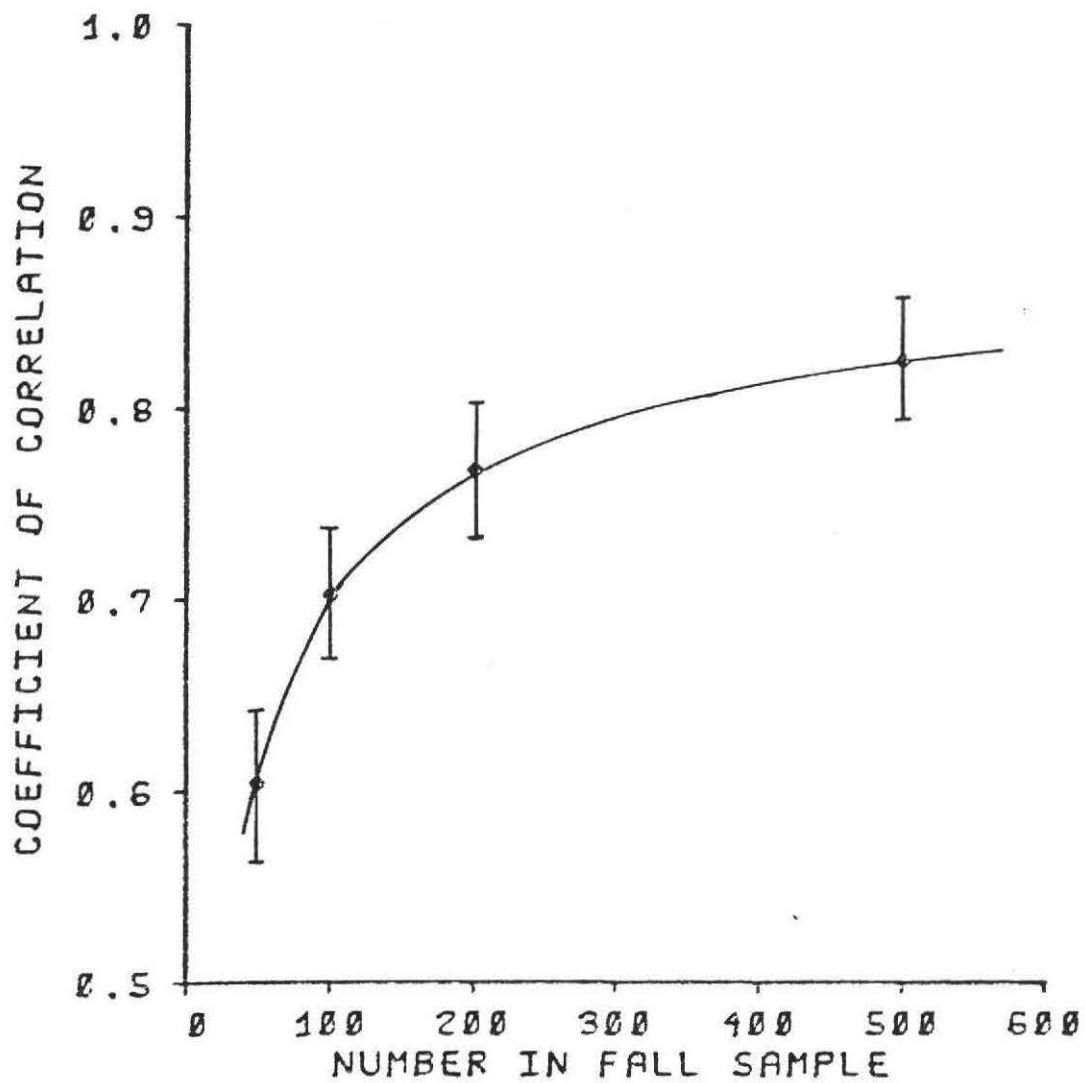


Figure 9. Coefficient of correlation between estimated fall proportion of fawns and spring rates of recruitment for various sizes of samples. The error bars represent 95 percent confidence intervals for 5 simulations.

The relationship shown in Figure 9 illustrates the importance of the size of the sample in the amount of correlation ( $r$ ) between the fall proportion of fawns and the spring rate of recruitment. With samples of 100 or fewer animals, estimates of fall proportions explained less than 50 percent ( $r^2$ ) of the variability in the spring recruitment rate of the simulated population; much less than the 73 percent explained when the fall proportions were known. For samples of 500 animals, the coefficient of correlation begins to approach that calculated when the fall proportion was known, but is still significantly less ( $P = 0.032$ , randomization test (Green, 1977)).

These coefficients of correlation between the fall proportion of fawns and the rate of recruitments of fawns into the population the following spring were tested to see if they were significantly less than 0.90 using the sign test (Ott, 1977). In all of the cases considered, including the case where the fall proportions of fawns were known, the correlation coefficients were found to be significantly less ( $P \leq 0.0312$ ) than 0.90. Thus, the hypothesis (H2) that there is a high correlation between the fall proportion of fawns and the rate of recruitment of fawns into the spring population must be rejected based on the criterion described in the methods section.

Although the testing of the hypothesis, H2, provided insights into the strength of the relationship between the fall proportion of fawns and the spring rate of recruitment, it did not indicate the reliability of using the fall proportion of fawns to predict spring recruitment rates. In an attempt to gain insights on this question, an investigation was made to evaluate the reliability of using the fall proportion of fawns to predict the spring recruitment rate. This was done by

calculating the 95 percent prediction interval around the spring recruitment rate for a given fall proportion of fawns.

The 95 percent prediction interval, calculated using linear regression techniques as described by Ott (1977), is a measure of how precisely the fall proportion of fawns can predict the rate at which fawns are recruited into the spring population. The narrower the prediction interval, the more reliable the fall proportion is as an indicator of recruitment. If the prediction intervals for two different fall proportions overlap, then they may not represent different spring recruitment rates.

The 95, 90, and 80 percent prediction intervals around the spring recruitment rate (expressed as fawns per doe) for different fall proportions of fawns are illustrated in Figure 10. These represent prediction intervals when the fall proportion of fawns is known. The prediction intervals were calculated from data from the first simulation that was used to test H2.

Two important points can be made concerning the prediction intervals around spring recruitment rates for given fall proportions of fawns illustrated in Figure 10. First, the fall proportion of fawns is not a precise indicator of the spring rate of recruitment. The wide 95 percent prediction intervals imply that only a gross indication of the spring recruitment rate may be obtained by using the fall proportion of fawns. Second, the fall proportion of fawns between two populations must differ by a relatively large amount (nearly 0.2) before one can conclude that they probably represent different spring recruitment rates. If the fall proportion of fawns is estimated from a sample, then this difference would probably have to be greater than 0.2.

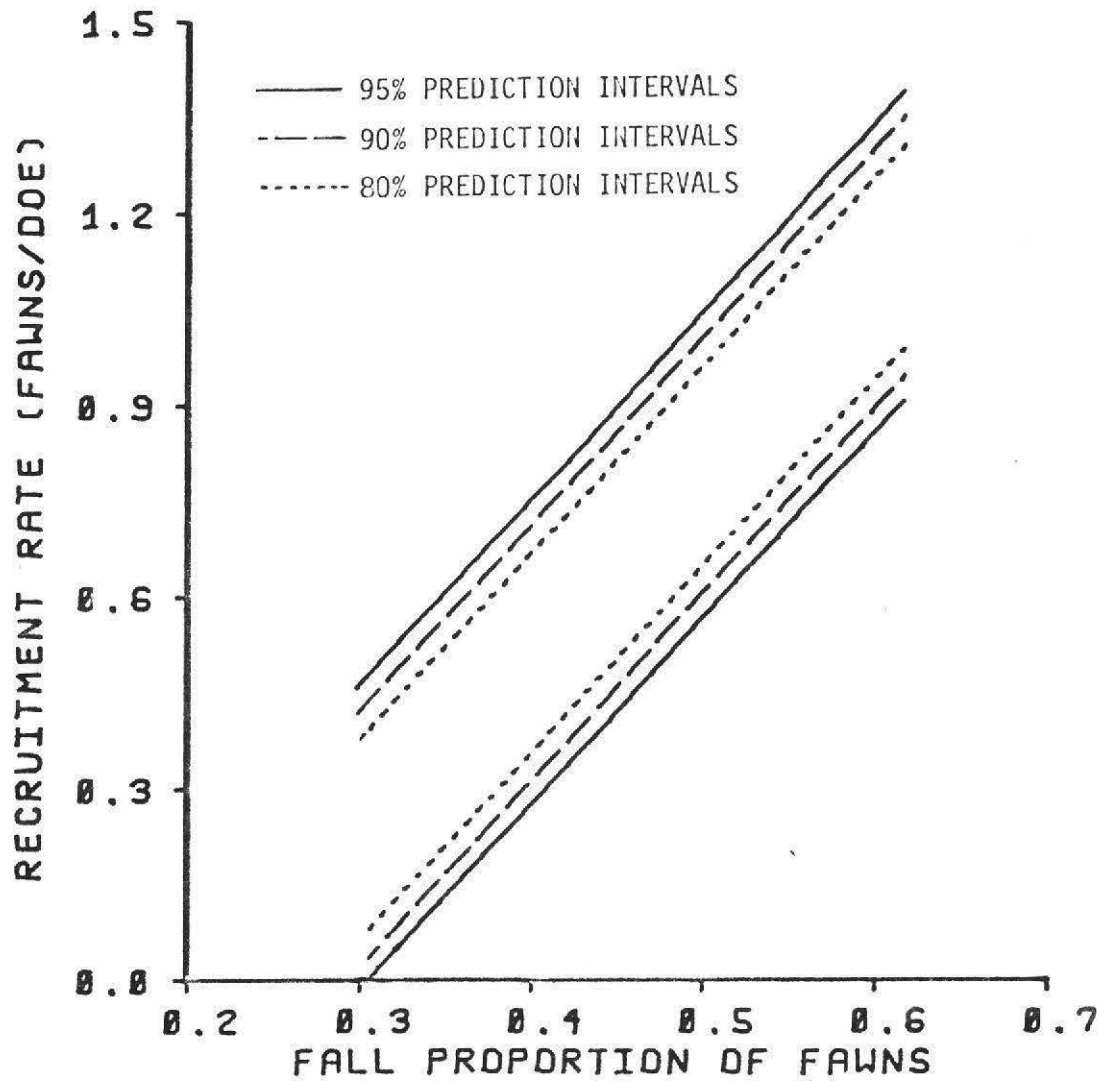


Figure 10. The 95 percent prediction intervals around the spring recruitment rate for the actual fall proportion of fawns.



As a tangent to this analysis, an attempt was made to provide a better index of the rate at which fawns are recruited into the spring population. As was shown earlier (equation (1), page 6), the fall proportion of fawns ( $P_f$ ) is related to the proportion of fawns in the population the following spring ( $P_s$ ) by the relationship

$$P_s = P_f \cdot S_f/S_t$$

where  $S_f$  is the survival rate of fawns over the winter and  $S_t$  is the weighted mean survival rate of all fawns and does over the winter. Since there is a one to one relationship between the proportion of fawns and the number of fawns per doe (Figure 1), knowledge of the survival rates  $S_f$  and  $S_t$ , in addition to the fall proportion of fawns ( $P_f$ ), should produce an index which is more highly correlated with the rate at which fawns are recruited into the spring population (expressed as the number of fawns per doe).

In an attempt to utilize the relationship expressed in (1),

$$\hat{P}_s = \hat{P}_f \cdot \hat{S}_f/\hat{S}_t \quad (15)$$

was used as an index for the rate of recruitment of fawns into the spring breeding population.  $\hat{P}_f$ ,  $\hat{S}_f$ , and  $\hat{S}_t$  represent estimates of the fall proportion of fawns ( $P_f$ ), the overwinter fawn survival rate ( $S_f$ ), and the weighted mean overwinter survival rate for all fawns and does ( $S_t$ ), respectively. The coefficients of correlation ( $r$ ) between the rate at which fawns are recruited into the spring population (expressed as the number of fawns per doe) and this index were calculated for mule deer populations simulated over a period of 1000 years.

Simulations were made using estimates of the proportion of fawns ( $\hat{P}_f$ ), the overwinter survival rate of fawns ( $\hat{S}_f$ ), and the weighted mean overwinter survival rate of all fawns and does ( $\hat{S}_t$ ) calculated from

samples of various sizes. Each of these estimates was assumed to have been obtained from binomial sampling and estimates used in the simulations were randomly selected from normal approximations to binomial distributions. This procedure simulated the estimation of overwinter survival rates ( $S_f$  and  $S_t$ ) that would be obtained from animals marked in the fall (such as with radio collars) whose status (alive or dead) was known in the spring. It was assumed that the estimates of  $P_f$ ,  $S_f$ , and  $S_t$  were independent of each other.

The coefficients of correlation between the rate at which fawns are recruited into the spring population and the index,  $P_s$ , are shown in Figure 11 for several simulations. Each datum point on the graph represents the mean correlation coefficient calculated from five simulations of a mule deer population over a period of 1000 years. Only information from 200 randomly selected years of the 1000-year simulations were considered in the calculation of each correlation coefficient. The 95 percent confidence intervals are shown for each estimated correlation coefficient. Simulations of 1000 years were made for cases where the overwinter survival rate  $S_f$  and  $S_t$  were each estimated from sample sizes of 25, 50, 100, and 250 animals and where the proportion of fawns in the fall population ( $P_f$ ) was known and where it was estimated from samples containing 200 fawns and does.

Two conclusions can be drawn from the results illustrated in Figure 11. First, as expected, estimates of the overwinter survival rate of fawns ( $S_f$ ) and the weighted mean overwinter survival rate of all fawns and does ( $S_t$ ) can be used with an estimate of the fall proportion of fawns ( $P_f$ ) to produce a better index of the rate at which fawns are recruited into the spring population than the proportion of

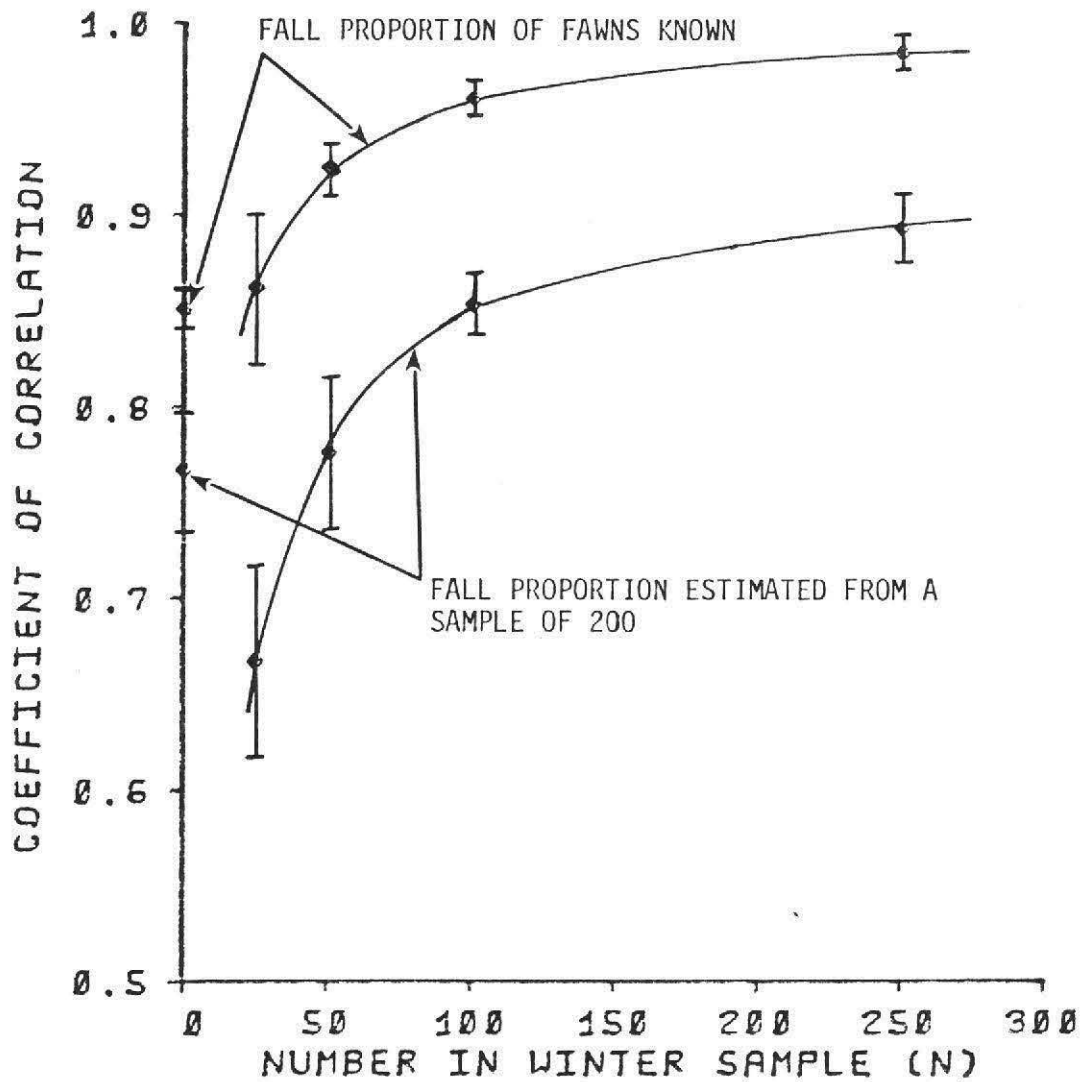


Figure 11. Coefficient of correlation between the rate of recruitment of fawns into the spring population and the index  $\hat{P}_S$ . The error bars represent 95 percent confidence intervals for 5 simulations. Points shown when  $N = 0$  represent the situations where the fall proportion ( $P_f$ ) was used as an index for recruitment.

fawns ( $P_f$ ) used alone. In the cases where the proportion of fawns in the fall,  $P_f$ , was estimated from samples of 200 fawns and does, the index,  $\hat{P}_S$ , was a significantly ( $P < 0.0005$ , randomization test) better index of the rate at which fawns were recruited into the spring breeding population than was the estimate of the proportion of fawns in the fall population,  $P_f$ , when the survival rates,  $S_f$  and  $S_t$ , were each estimated from a sample of 100 or more individuals. When the proportion of fawns in the fall population ( $P_f$ ) was known, the index  $\hat{P}_S$  using estimates of the survival rates,  $S_f$  and  $S_t$ , each calculated from samples of 50 or more individuals was a significantly ( $P < 0.01$ , randomization test) better indicator of the recruitment of fawns into the spring population than was the fall proportion of fawns,  $P_f$ . These results indicate that the larger the sample size used to estimate the fall proportion of fawns ( $P_f$ ), the smaller the number of individuals needed to estimate the survival rates  $S_f$  and  $S_t$  to produce an index ( $\hat{P}_S$ ) which is significantly better than an index using just an estimate of the fall proportion of fawns  $P_f$ .

The second conclusion that can be drawn from this analysis is that if estimates of the survival rates,  $S_f$  and  $S_t$ , are made from sample sizes that are too small, the index  $\hat{P}_S$  may actually be a worse indicator of the rate at which fawns are recruited into the spring population than is an estimate of the fall proportion of fawns,  $P_f$ . For the case where the fall proportion of fawns,  $P_f$ , was estimated from a sample of 200 fawns and does and the survival rates,  $S_f$  and  $S_t$ , were each estimated from samples of only 25 individuals, the proportion of fawns,  $P_f$ , was a significantly ( $P < 0.0005$ , randomization test) better index of the recruitment of fawns than was the index,  $\hat{P}_S$ . This would be

expected as small sample sizes would produce large variances in estimates of the survival rates  $S_f$  and  $S_t$  and reduce the reliability of the index,  $\hat{P}_S$ .

#### Fall Proportion of Fawns as Index of Reproductive Performance

The model used to simulate a population of mule deer described in the methods section was also used to investigate the reliability of using the fall proportion of fawns as an indicator of the reproductive performance of a population. As defined earlier, the reproductive performance of a population refers to the number of fawns produced per doe 2 or more years of age that are alive at a specified time. The number of fawns surviving until October was used in this analysis.

The coefficients of linear correlation ( $r$ ) between the fall proportion of fawns and the number of fawns produced per doe 2 or more years of age surviving to October are shown in Table 8 for ten different 1000-year simulations of the population. The mean and 95 percent confidence intervals around the mean are shown for the correlation coefficients. A scattergram depicting the relationship between the fall proportion of fawns and the number of fawns produced per doe two or more years of age surviving to October is shown in Figure 12. The values shown in the figure were obtained from a sampling of values from the first of the ten simulations.

From the ten simulations, the coefficient of correlation ( $r$ ) ranged from 0.879 to 0.903 with a mean of 0.888. This means that approximately 79 percent ( $r^2$ ) of the variability in the reproductive performance measured in October could be accounted for by the fall proportion of fawns.

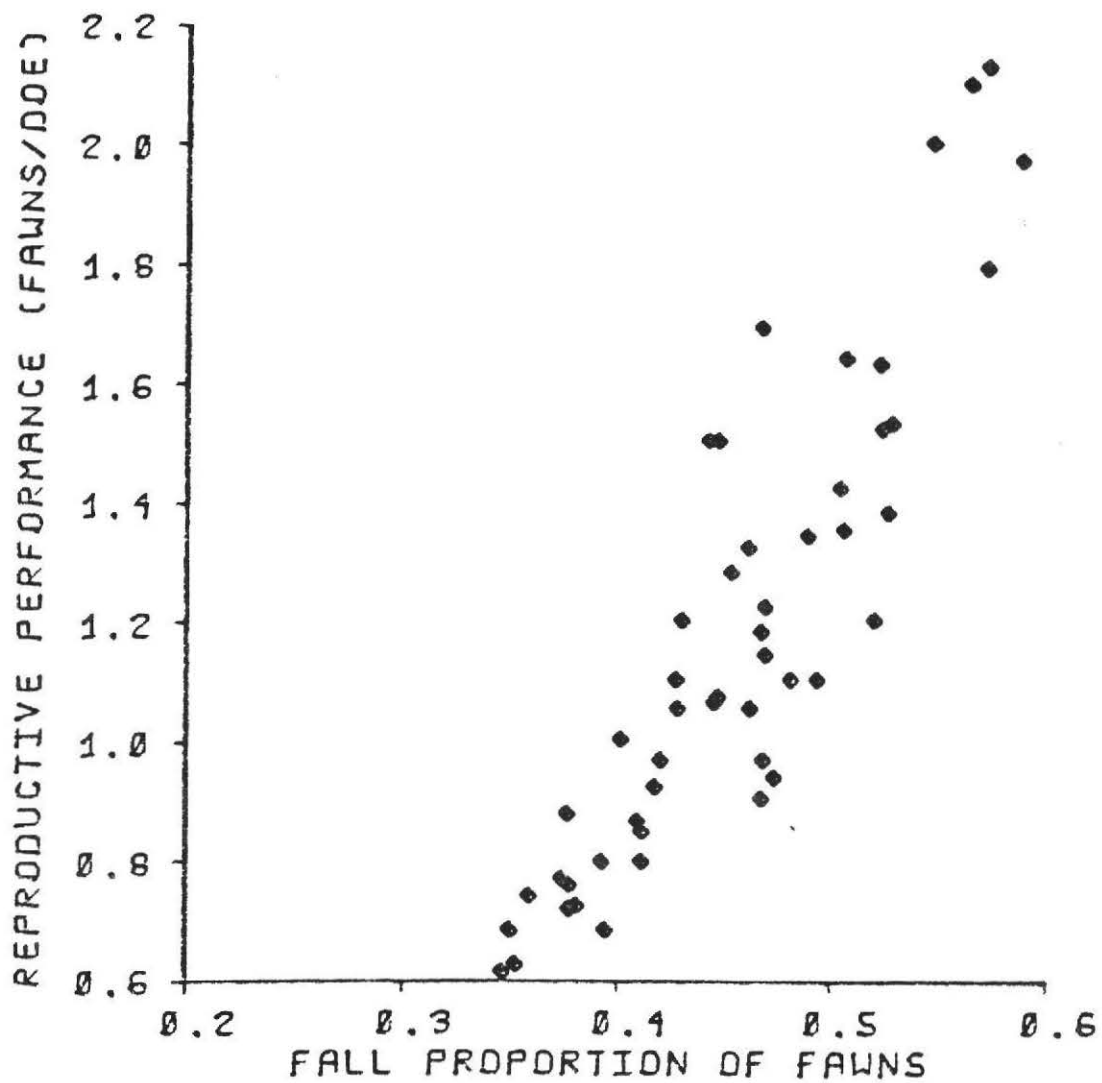


Figure 12. Scattergram showing relationship between the proportion of fawns in the fall and the reproductive performance of the population.

As was discussed in the previous section, the fall proportion of fawns is usually estimated from binomial sampling of the fawns and does in the population. The effect of the sample size used to estimate this proportion on the correlation between the reproductive performance and the proportion of fawns in the fall population was investigated for sample sizes of 50, 100, 200, 350, and 500. Five simulations of the mule deer populations of 1000 years each were made for each sample size. Values from 200 randomly selected years from each 1000-year simulation were used to calculate coefficients of correlation between the proportion of fawns and the reproductive performance of the population.

The coefficients of linear correlation for these simulations are depicted in Figure 13. The mean correlation coefficients calculated for the cases where the proportion of fawns were estimated from 50, 100, 200, 350, and 500 fawns and does were 0.629, 0.724, 0.789, 0.828, and 0.850, respectively. When samples of 500 fawns and does are used to estimate the proportion of fawns, the correlation coefficient approaches that calculated when the fall proportion of fawns is known but is still significantly less ( $P = 0.001$ , randomization test).

These correlation coefficients were used to test the hypothesis (H3) that the proportion of fawns in the populations of fawns and does were highly correlated with the reproductive performance of the population. The correlations calculated when the fall proportion of fawns was known, while close to 0.90, are significantly less ( $P = 0.0098$ , sign test) than this value. Similarly, the correlation coefficients calculated when estimates were made of the proportion of fawns are also significantly less ( $P = 0.03$ , sign test) than 0.90. Thus, the hypothesis (H3) that there is a high correlation between reproductive

performance and the proportion of fawns in the fall population must be rejected based on the criterion established in the methods section. These results indicate that the proportion of fawns among fawns and does in the fall population is not a highly reliable indicator of the reproductive performance of a population in the fall. However, if it is used as an indicator of the reproductive performance, estimates of the proportion of fawns should be made from relatively large sample sizes.

As was the case in the testing of hypothesis H2, the testing of the hypothesis H3 was designed to provide insights into the strength of the relationship between the fall proportion of fawns and a measure of productivity. It was not designed, however, to investigate the reliability of using the fall proportion of fawns to predict the reproductive performance of a population as measured in the fall. In an attempt to evaluate the reliability of using the fall proportion of fawns to predict the reproductive performance, the 95, 90, and 80 percent prediction intervals around the reproductive performance for a given fall proportion of fawns were calculated. These intervals are shown in Figure 14 for the situation when the fall proportion of fawns is known.

Two important points are evident from the relationship shown in Figure 14. First, the wide 95 percent prediction intervals imply that only gross indications of the reproductive performance may be obtained by using the fall proportion of fawns. Precise indications of the reproductive performance cannot be made because of the large amount of uncertainty in the predicted reproductive performance for a given fall proportion of fawns. Second, the fall proportion of fawns between two populations may differ by a relatively large amount (nearly 0.15)



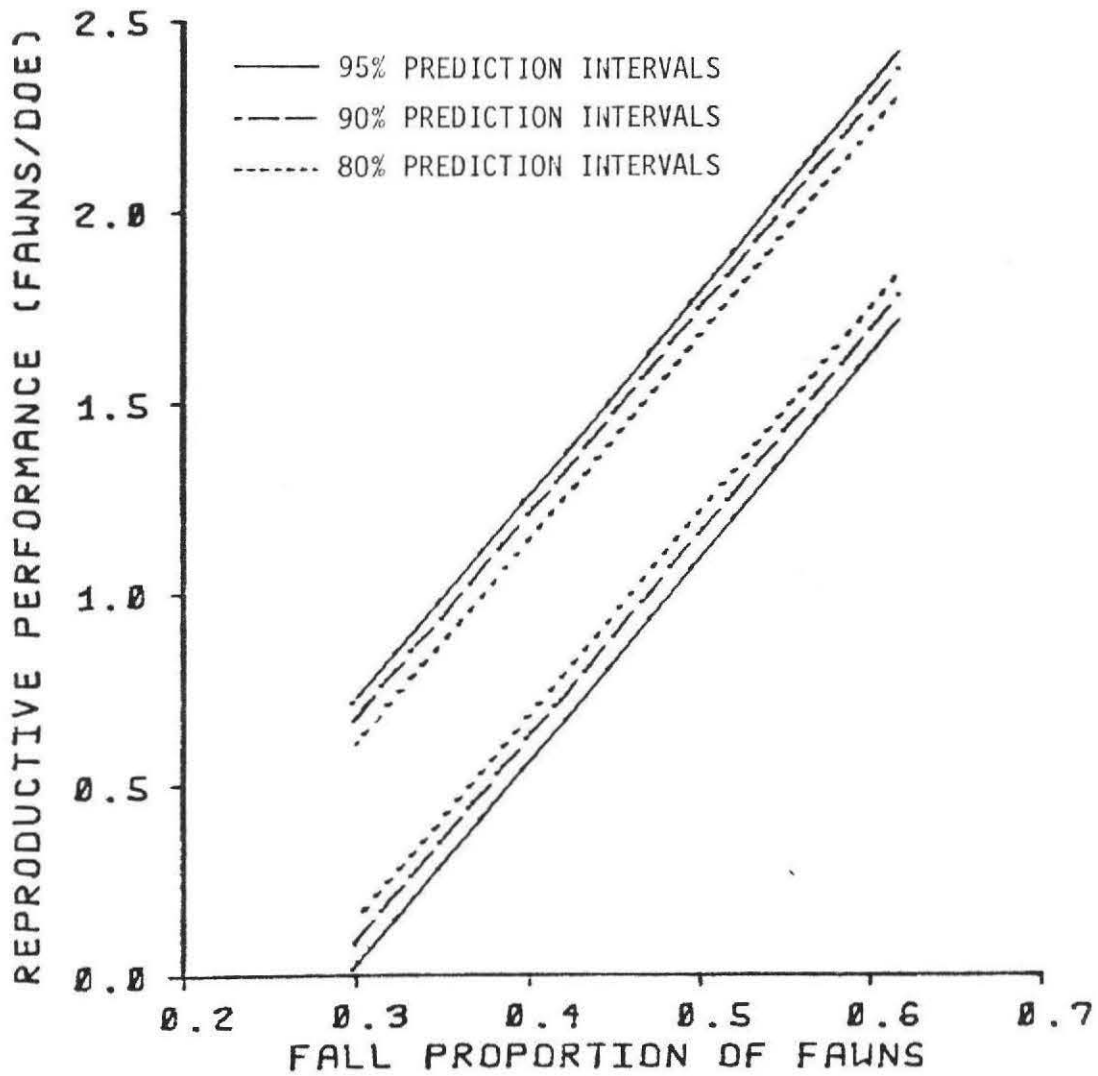


Figure 14. The 95 percent prediction intervals around the reproductive performance for the actual fall proportion of fawns.

before one can conclude that they probably represent different reproductive performances.

## CONCLUSIONS AND RECOMMENDATIONS

### Indices of Productivity

Measures of the productivity of mule deer populations are important quantities for effective management. The proportion of fawns has frequently been used as a measure or index of productivity of mule deer populations. This study has evaluated, in part, the reliability of using the proportion of fawns as indicators of two measures of productivity, recruitment of fawns into the spring population and reproductive performance.

The correlation coefficients ( $r$ ) calculated from a simulated mule deer population for the relationship between the fall proportion of fawns and the rate at which fawns are recruited into the spring population indicate that a significant ( $r = 0.856$ ,  $P \ll 0.001$ ) relationship exists between these two quantities. Similarly, these simulations of a population of mule deer indicate that a significant ( $r = 0.888$ ,  $P \ll 0.001$ ) relationship exists between the fall proportion of fawns and the reproductive performance of the population measured in the fall. Despite these significant relationships, the fall proportion of fawns explains less than 80 percent of the variability in each of these measures of productivity.

It was shown through regression analyses that the fall proportion of fawns is not always a reliable indicator of the rate at which fawns are recruited into the spring population or the reproductive performance of a population. Because of the variability in the dynamics of

a population, there is not a one-to-one relationship between the proportion of fawns and these measures of productivity. Only gross indications of these measures of productivity can be obtained by using the fall proportion of fawns. Differences in the spring rates of recruitment or reproductive performance between two populations can be inferred only when the differences in their fall proportion of fawns are relatively large (0.15 or greater).

Because the fall proportion of fawns is not always a reliable indicator of these measures of productivity, managers should not rely on the proportion of fawns in the fall as the only indicator of the productivity of a mule deer herd. Other indicators of the population's productivity and condition (such as harvest rates, pregnancy rates, physical condition of the deer, and range condition) should be considered as well. The results obtained by several indices should then be evaluated to assess the productivity of a herd.

If the fall proportion of fawns is to be used as an indicator of recruitment into the spring population or reproductive performance, then estimates of this quantity should be made from relatively large samples of fawns and does. Results from the mule deer simulations in this study suggest that samples of nearly 500 fawns and does produce estimates of the proportion of fawns whose correlations approach those calculated when the proportion of fawns is known, the optimum situation. Variability due to random sampling errors significantly reduce these correlations and the reliability of this index when sample sizes are small, particularly below 100 fawns and does.

Even when the fall proportion of fawns is known, the amount of correlation between this proportion and the recruitment of fawns into

the breeding population the following spring is limited by the variability in the overwinter survival rates of fawns and does. As expected, estimates of these survival rates can be used with an estimate of the proportion of fawns in the fall to produce an index of the recruitment of fawns which is significantly better than just an estimate of the proportion of fawns. A major problem with this index, however, is the sample size of fawns and does needed to produce significantly better indices of recruitment. If estimates of these survival rates are made from deer marked in the fall whose status (alive or dead) was determined in the spring, then 100 or more individuals must be marked and relocated to produce a significantly better index. The cost of capturing and marking in the fall and then relocating in the spring 100 fawns and does would most likely be prohibitive, particularly on an annual basis. Thus, unless estimates with small variances of the overwinter survival rates of fawns and does can be made less expensively using a different estimation scheme, this index cannot be realistically utilized.

Another indicator of the rate of recruitment of fawns into the breeding population which may be significantly better than the fall proportion of fawns is an estimate of the proportion of fawns (nearly one year old) in the spring population. This estimate would provide a direct measure of the rate at which fawns enter the breeding population without being confounded by the differential overwinter survival of fawns and does. Ideally, these estimates should be obtained when fawns can be differentiated from does with considerable accuracy and when the period of differential rates of survival has passed. Such conditions may exist in late March, just before the animals leave the wintering ground. While the animals occur in herds, rather than as scattered

individuals, it may be possible to distinguish fawns from does with careful observations. Further field work is necessary to address these possibilities.

The variability which reduces the correlation between the fall proportion of fawns and the reproductive performance of the population in the fall is predominately due to the number of yearling does present in the population. The yearling does, which produce very few fawns, reduce the average number of fawns per doe when they are numerous in the population. An estimate of the relative number of yearlings in a population can be useful when interpreting this index of reproductive performance. If there are few yearlings, then the proportion of fawns should reflect, quite accurately, the reproductive performance of a population. If, however, there are relatively large numbers of yearling does in the population, then the proportion of fawns would be expected to underrate the reproductive performance of the population.

#### Misclassification

Hanson (1963) suggests that the misclassification of fawns and does will bias estimates of the proportion of the population which are fawns. The work completed in this study indicates that the misclassification of fawns will bias estimates of the proportion of fawns. The amount of bias is a function of the probabilities of misclassifying a fawn as a doe, misclassifying a doe as a fawn and the actual proportion of fawns in the population of fawns and does. The average amount of bias due to misclassification is independent of the size of the sample of fawns and does. Larger samples will only produce biased estimates with small variances.

The problem of misclassifying fawns and does is probably most serious when the actual proportion of fawns is low. In this situation, the misclassification of some of the relatively large number of does will add a sizable number of "fawns" to the actual number counted. This will cause the estimate of the proportion of fawns to be somewhat greater than it actually is. The overestimation of the proportion of fawns, when the fawn production is low, may lead to some management decisions which will be harmful to the population.

Much of the problem in interpreting estimated fawn proportions, due to misclassification, is a result of the bias being quite unpredictable. The bias may be positive, negative, or even zero depending on the probabilities of misclassification of fawns and does and the proportion of fawns (see Figure 4). Unless the probabilities of misclassification are known, the amount of bias is impossible to determine. Thus, its effect on specific estimators or indices which utilize the proportion of fawns is not known and the reliability of these quantities becomes questionable.

The next step in evaluating the problem of misclassification should be to design field studies to determine whether or not the misclassification of fawns and does is a frequent phenomenon and a problem worth serious consideration. These studies could be patterned after the work of Downing (1970) on white-tailed deer where he attempted to determine the percent of small antlered bucks which were misclassified as does. Also, the development of a theoretical model, similar to the one presented here, which would include the misclassification of bucks would be useful in evaluating the effect of all types of misclassification. Whether or not these studies are undertaken, the results from

this study indicate that biologists classifying herds of mule deer should use great care in classifying each individual observed.

#### Concluding Remarks

The work discussed in this thesis is not designed to be the final word concerning the use of fall proportions of fawns as an indicator of productivity and the effects of misclassifying fawns and does on estimates of the proportion of fawns. Instead, it was designed to be an objective evaluation of some aspects of these problems as they apply to mule deer populations in the Intermountain West. Extrapolations of these results to other species of large mammals should be done with care as different life strategies may result in somewhat different conclusions. Ideally, this type of analysis should be done for all species where the proportion of young in the population is used as an indicator of the productivity of the population.



## SUMMARY

1. Historically, the relationship between the number of fawns and does, expressed as a ratio or fraction, has been important in attempts to characterize populations of mule deer.
2. The misclassification of fawns and does produces biased estimates of the proportion of fawns when calculated from counts of does and fawns obtained from sampling which is binomial in nature. The amount of bias is a function of both levels of misclassification of fawns and does and the actual proportion of fawns. This bias is unpredictable unless the levels of misclassification are known. It may result in circumstances wherein the actual proportion of fawns does not fall within the range of estimates produced by the majority of samples. The misclassification of does as fawns can result in large overestimations of the proportion of fawns when fawns are relatively few in number.
3. The fall proportion of fawns was found to be a gross indicator of the rate at which fawns are recruited into the spring population. Correlations between the proportion of fawns in the fall and the rate of recruitment into the spring population were found to be approximately 0.86 for a simulated population of mule deer when the fall proportion was known. Correlations between estimates of the fall proportion and the spring recruitment are

significantly less than when the fall proportion is known. This correlation increases with the sample size used to estimate the fall proportion. Differences in the spring rate of recruitment between two populations can be inferred only when their fall proportion of fawns differ by approximately 0.20.

4. Estimates of the survival rates of fawns and does can be used in conjunction with estimates of the fall proportion of fawns to provide a better index of the spring rate of recruitment than the estimated fall proportion of fawns used alone. However, the sizes of samples needed in the estimation of these survival rates are probably too large to be obtained on an annual basis (see Figure 11).
5. The fall proportion of fawns was found to be a gross indicator of the reproductive performance of a population. Reproductive performance was defined as the number of fawns produced per doe aged 2 years or older which survived to the fall. The correlation between the fall proportion of fawns and the reproductive performance were found to be approximately 0.89 for a simulated population when the fall proportion of fawns was known.

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APPENDICES

APPENDIX A

Population Model Used in Tables 1 and 2



The ratio of fawns to does and the proportion of fawns shown in Tables 1 and 2 of the main text were calculated from data generated by the projection matrix model shown in Figure A1. The model was used to predict the population in the fall after the hunting season from the population in the previous fall after the hunting season. It represents only the female segment of a population where both sexes are harvested.

$$\begin{bmatrix}
 a_1 & a_2 & a_3 & a_4 & a_5 & a_6 & a_7 & a_8 \\
 s_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & s_2 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & s_3 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & s_4 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & s_5 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & s_6 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & s_7 & 0
 \end{bmatrix}
 \begin{bmatrix}
 n_1 \\
 n_2 \\
 n_3 \\
 n_4 \\
 n_5 \\
 n_6 \\
 n_7 \\
 n_8
 \end{bmatrix}
 =
 \begin{bmatrix}
 n_1 \\
 n_2 \\
 n_3 \\
 n_4 \\
 n_5 \\
 n_6 \\
 n_7 \\
 n_8
 \end{bmatrix}$$

Projection Matrix
Popn. in
Popn. in  

Year i
Year i+1

Figure 15. Projection matrix model of mule deer populations with 8 age classes.

The  $a_i$  represent the number of female fawns that reach the fall, post-hunting population produced per female in age class  $i$  that were alive in the previous fall, post hunting season. The  $s_i$  are the values for survival of females from age class  $i$  to age class  $i + 1$ . They were calculated for each population from the combination of non-hunting and hunting rates of mortality; during the hunting season,

only mortality from hunting was assumed to occur. These rates of mortality and the rates of fawn production are shown in Tables 1 and 2 of the main text.

The populations were assumed to have a stationary age structure each fall following the hunting season; that is, they had the same number of individuals and proportions of the total population in each age class each fall following the hunting season. These stationary age structures are shown in Tables A1 and A2 for the populations referred to in Tables 1 and 2, respectively, of the main text. Also shown are the same populations just prior to the hunting season from which the ratio of fawns to does and proportion of fawns were calculated. The post-hunting populations are such that the total number of females sums to 1000.

Shown below is an example of how the ratio of fawns to does, proportion of fawns in the population, and net productivity were calculated. The population used in this example is population 4 of Table 2 of the main text and Table A2 of this appendix.

Let:

$$TD = \text{Total number of does} = \sum_{i=2}^8 \text{number of does in age class } i = 837$$

$$TFF = \text{Total number of female fawns} = 306,$$

then:

$$TF = \text{Total number of fawns} = TFF \times 2 = 612$$

and

$$\text{Ratio of fawns to does} = TF/TD = 612/837 = \underline{.731}$$

and

$$\text{Proportion of fawns} = TF/(TF + TD) = 612/(612 + 837) = \underline{.422}.$$

Table 9. The populations referred to in Table 1 just before and just after the fall hunting season. All age classes are harvested with equal intensity.

Popn.	Age class								Total
	1	2	3	4	5	6	7	8	
	<u>After Hunting Season</u>								
1	278	208	156	117	88	66	50	37	1000
2	278	208	156	117	88	66	50	37	1000
3	278	208	156	117	88	66	50	37	1000
4	278	208	156	117	88	66	50	37	1000
	<u>Before Hunting Season</u>								
1	278	208	156	117	88	66	50	37	1000
2	291	219	164	123	92	69	52	39	1049
3	306	229	172	129	97	72	54	41	1100
4	319	239	179	135	101	76	57	43	1149

Table 10. The populations referred to in Table 2 just before and just after the fall hunting season. Age classes 2 to 8 are harvested with equal intensity while age class 1 is not harvested.

Popn.	Age class								Total
	1	2	3	4	5	6	7	8	
	<u>After Hunting Season</u>								
1	278	208	156	117	88	66	50	37	1000
2	288	212	157	115	85	63	46	34	1000
3	297	216	156	114	83	60	43	31	1000
4	306	219	156	112	80	57	41	29	1000
	<u>Before Hunting Season</u>								
1	278	208	156	117	88	66	50	37	1000
2	288	227	167	123	91	67	49	36	1048
3	297	245	178	129	94	68	49	36	1096
4	306	264	189	135	96	69	49	35	1143

Let:

$$\begin{aligned} TP &= \text{Total number of does just prior to hunting season} \\ &= \sum_{i=1}^8 \text{ number of does in age class } i = 1143, \end{aligned}$$

then

$$\begin{aligned} TH &= \text{Total number of does to be harvested} \\ &= \text{Number of does in post-hunt stationary population} \\ &= 1143 - 1000 = 143 \end{aligned}$$

and

$$\text{Net productivity} = TH/TP = 143/1143 = \underline{.125}.$$

## APPENDIX B

Calculation of the Expected Values and Variances  
for the Estimators  $\hat{P}$  and  $\hat{P}^*$

The expected values and variances of  $\hat{P}$  and  $\hat{P}^*$  were used in the testing of H1 and subsequent analysis. They were determined as follows.

When sampling a population of fawns and does with replacement where each individual has an equal probability of being observed (binomial sampling) and when no misclassification occurs, the probability that an observed individual is counted as a fawn is simply  $P$ , where  $P$  is the actual proportion of fawns in the population of fawns and does. The probability an observed individual is counted as a doe is  $1-P$ . If  $f$  fawns are counted in a binomial sample containing  $n$  fawns and does, then  $\hat{P} = f/n$  is an unbiased estimate of the proportion of fawns with an expected value of  $P$  and a variance of  $P(1 - P)/n$  (Cochran, 1963).

To determine the probability an observed individual in binomial sampling is a fawn when misclassification occurs, the levels of misclassification of does as fawns and fawns as does must be specified. Let  $P_{fd}$  be the proportion of does misclassified as fawns and  $P_{df}$  be the proportion of fawns misclassified as does.  $P_{fd}$  would thus represent the conditional probability that an observed individual is counted as a fawn given that it actually is a doe while  $1 - P_{fd}$  is the conditional probability that an observed individual is counted as a doe given that it actually is a doe. Similarly,  $P_{df}$  would be the conditional probability that an observed individual is counted as a doe when it actually is a fawn and  $1 - P_{df}$  would be the conditional probability a fawn is counted as a fawn. Then letting  $P_{ff} = 1 - P_{df}$ , the probability an individual observed at random is counted as a fawn is  $P \cdot P_{ff} + (1 - P) \cdot$

$P_{df}$  (Freund, 1971, p. 54) where  $P$  is the actual proportion of fawns in the population of fawns and does. Similarly, the probability an individual is counted as a doe is  $(1 - P) \cdot P_{dd} + P \cdot P_{df}$ . Thus, in a binomial sample containing  $n$  fawns and does where  $f$  are counted as fawns and  $d$  are counted as does,  $\hat{P}^* = f/n$  would be an estimate of the proportion of fawns with an expected value of  $P^*$  and a variance of  $P^* \cdot (1 - P^*)/n$  where  $P^* = P \cdot P_{ff} + (1 - P) \cdot P_{fd}$  (Cochran, 1963).



## APPENDIX C

Verification and Validation, Parameter and Variable List,  
and FORTRAN Code for the Model Used  
to Test H2 and H3

### Model Verification and Validation

Verification of the model of a population of mule deer (MULEDEER) used to test the hypotheses H2 and H3 was done in three major steps. First, the FORTRAN code of each component of MULEDEER was debugged using the FORTRAN compiler on the Burroughs 6700 computer. This was a necessary procedure each time a change in the FORTRAN code was made. Second, short programs were written to obtain output values from individuals or groups of subroutines which were compared with values calculated on a hand calculator.

In the third step, verification on the complete model was done. This involved two major tests. In the first test, simulations of 100 years were made where the mean birth and survival rates for each class were used each year. The stable age structure, fall proportion of fawns, reproductive performance and spring rate of recruitment in the last year of the simulation were compared with values calculated with a hand calculator.

In the second test, several simulations over a 1050-year period were made with the birth and survival rates varying randomly as described in the methods section. The average exponential rate of increase for the population was calculated over the last 1000 years of the simulation. Since the mean rates were designed to produce a population which is stable in size, the population with rates randomly selected from uniform distributions should have an average exponential rate of increase near zero. In the simulations made, the average rates of increase ranged from -0.012 to 0.003 which represent an average

annual rate of change of the population of less than 1.2 percent per year. The majority of the average annual rates of increase for the 1050-year simulations were slightly less than zero, a phenomenon which agrees with analyses by Boyce (1977) on similar matrix models.

Validation of the model used to test the hypotheses H2 and H3 (MULEDEER) was done by comparing output from the model with data collected in the field. Specifically, the fall proportions of fawns calculated by the model were compared with estimates obtained from the classification of mule deer in Utah. The range of fall proportions of fawns generated during the 1050-year simulations (0.274 to 0.591) compared favorably with those listed (0.194 to 0.603) by Day (1979) for herds of mule deer in Utah from 1970 to 1978 for both pre- and post-hunting season composition counts. The upper value (0.603) is not significantly different ( $P > 0.05$ , t test) from 0.591 for the sample classified, while the lower value (0.194) obtained from a pre-hunting season sample of 115 fawns and does is significantly ( $P < 0.05$ , t test) less than the low value from the model (0.274). A sample of 259 fawns and does taken after a buck-only hunt, however, produced an estimate of the proportion of fawns of 0.363, a value which is higher than the minimum produced by the model. The next lowest value reported by this report was 0.239, estimated from a sample of 159 fawns and does. This was not significantly ( $P > 0.05$ , t test) different from the lowest value produced by the model.

Ideally, other comparisons with model output and data collected in the field should have been made to provide a more complete model validation. Highly reliable data on other population parameters (e.g., age structure, rate of increase, recruitment rates) from field

populations, however, does not exist for mule deer. As a result, comparisons between the model output and other types of data characterizing populations of mule deer could not be made. The maximum rate of increase in one year that was observed to be generated by the model (42 percent), however, was found to be well within the levels found for white-tailed deer by McCullough (1979) on the George Reserve in Michigan.

A complete sensitivity analysis of the population model used to test hypotheses H2 and H3 was not undertaken. Such an analysis would include a calculation of the changes in the coefficients of correlation (calculated for the relationships between the fall proportion of fawns and spring rate of recruitment and the fall proportion of fawns and reproductive performance) when the input parameters of the model were changed by specified amounts. This would provide insights into the accuracy that would be desirable for the input parameters. Also, such an analysis would provide additional insight into the validity of the conclusions obtained from the simulations and would to an extent examine the applicability of the model to other ungulate species with similar life history strategies.

Changes in the coefficients of correlation as a result of changes in parameter values were superficially investigated for a few of the input parameters (specifically the mean birth rates for each age class). However, because the analysis was incomplete and cursory in nature, it did not warrant inclusion in this work.

#### Parameter and Variable List

The following is a list of the input parameters with FORTRAN name, definition, units, and value used in the model, MULEDEER, used

to test hypotheses H2 and H3. The source of these values is discussed in the methods section of the main text.

<u>FORTTRAN</u>	<u>Definition</u>	<u>Units</u>	<u>Value</u>
FEC(i)	Mean number of fawns produced per doe of age i (fecundity)	fawns/does	i=1: 0.013 i=2: 0.975 i=3+: 1.610
SS(i)	Mean proportion of deer surviving from May to October in age class i	-	i=1: 0.720 i=2: 0.910 i=3+: 0.910
SW(i)	Mean proportion of deer surviving from October to May in age class i	-	i=1: 0.635 i=2: 0.790 i=3+: 0.857
FECPC(i)	Value used to specify range of fecundity rates for a doe in age class i	fawns/does	i=1: 0.013 i=2: 0.255 i=3+: 0.320
SSPC(i)	Value used to specify range of survival proportions from May to October in age class i	-	i=1: 0.170 i=2: 0.050 i=3+: 0.050
SWPC(i)	Value used to specify range of survival proportions from October to May in age class i	-	i=1: 0.235 i=2: 0.110 i=3+: 0.050
NFALL	Number of deer in fall sample	deer	≥ 1
NWINT	Number of deer in winter sample	deer	≥ 1

The following is a list of the important variables calculated in the model of a population of mule deer (MULEDEER).

<u>FORTTRAN</u>	<u>Definition</u>	<u>Units</u>
AN(i)	Relative number in age class i	deer
TFALL	Relative size of population of fawns and does in October	deer
TSPR	Relative size of population of fawns and does in May	deer
FFDR	Proportion of fawns in the October population	-

<u>FORTTRAN</u>	<u>Definition</u>	<u>Units</u>
RPRE	Reproductive performance of the population in October	fawns/doe
SFDR	Number of 1-year old fawns per doe in May population	fawns/doe
FAWN	Number of fawns produced per doe aged 2 or more years	fawns/doe
R	Exponential rate of increase of the population from one year to the next	-
SUMR	Average exponential rate of increase of the population for entire simulation.	-

Listing of Program MULEDEER,  
Sample 'Run' and  
Sample Output

```

C**** PROGRAM MULEDEER IS A PROJECTION MATRIX MODEL OF A MULE DEER
C POPULATION. THIS PROGRAM CALCULATES THE FALL PROPORTION OF
C FAWNS (FFDR), SPRING RECRUITMENT RATES (SFDR), REPRODUCTIVE
C PERFORMANCE (RPRE), AND RATE OF INCREASE (R) FOR THE
C POPULATION FOR A SPECIFIED NUMBER OF YEARS (NYRS). THESE
C VALUES ARE CALCULATED FOR THE POPULATION AFTER AN INITIAL
C 50 YEAR SIMULATION TO REMOVE THE EFFECTS OF THE INITIAL
C STABLE AGE STRUCTURE. ALL OF THE FAWNS UP TO 1 YEAR OF AGE
C AND THE FEMALE PORTION OF THE POPULATION OVER 1 YEAR OF
C AGE ARE CONSIDERED. THE POPULATION IS PREDICTED TWICE EACH
C**** YEAR: IN OCTOBER (FALL) AND IN MAY (SPRING).
COMMON/AA1/II,SS(12),SW(12),FEC(12),AN(12),NYRS
COMMON/AA2/SSM(12),SWM(12),FECM(12)
COMMON/AA3/SSPC(12),SWPC(12),FECPC(12)
COMMON/BB1/TFALL,FFDR,TSPR,SFDR,NFALL,NWINT,RPRE,FAWN,IXX,IYY
COMMON/CC1/S(12),F(12)
DOUBLE PRECISION DSEED
C.... THIS READS IN USER SPECIFIED OPTIONS AND INITIAL RANDOM NUMBER
C.... (DSEED).
WRITE(6,200)
READ(5,/) DSEED
KKX=1
WRITE(6,204)
READ(5,100) IYY
IF (IYY.EQ.1HN) GO TO 10
WRITE(6,205)
READ(5,/) NFALL
10 WRITE(6,206)
READ(5,100) IXX
IF (IXX.EQ.1HN) GO TO 11
WRITE(6,207)
READ(5,/) NWINT
11 CONTINUE
C.... INPUT PARAMETERS FOR THE POPULATION ARE READ IN.
CALL INPUT
DO 7 I=1,II
C.... FECUNDITY RATES ARE CHANGED TO NUMBER OF FEMALES PRODUCED
C.... PER DOE.
7 FEC(I)=FEC(I)/2.
C.... A MATRIX PREDICTING POPULATION CHANGES FROM SPRING TO
C.... SPRING IS CONSTRUCTED.
DO 6 I=1,II-1
F(I)=FEC(I)*SW(I)*SS(I)
IF(I.EQ.II) GO TO 6
6 S(I)=SW(I)*SS(I)
C.... THE PRINCIPLE EIGANVALUE OF THE ABOVE MATRIX IS CALCULATED.
CALL PREIG(II,PEV)
WRITE(6,201) PEV
C.... THE INITIAL STABLE AGE DISTRIBUTION IS CALCULATED FOR THE
C.... POPULATION IN THE SPRING.
CALL STABLE(PEV)
C.... THE POPULATION IS SIMULATED OVER AN INITIAL 50 YEARS.
DO 1 I=1,50
CALL LIMITS(KKX,DSEED)
CALL FALL(DSEED)
CALL SPRING(DSEED)
DO 2 J=1,II
2 AN(J)=AN(J)/TSPR
IF(I.EQ.50) TSPRA=1.-AN(1)
1 CONTINUE

```



```

SUMR=0.0
C.... THE POPULATION IS SIMULATED OVER THE SPECIFIED NUMBER OF
C.... YEARS (NYRS).
      DO 3 I=1,NYRS
        CALL LIMITS(KKX,DSEED)
        CALL FALL(DSEED)
        CALL SPRING(DSEED)
C.... THE RATE OF INCREASE OF THE POPULATION IS CALCULATED FROM THE
C     TOTAL SPRING POPULATION AGED 1 YEAR OR MORE (TSPR-AN(1)) AND
C     THE TOTAL SPRING POPULATION AGED 1 YEAR OR MORE FROM THE
C.... PREVIOUS YEAR (TSPRA).
      R=ALOG((TSPR-AN(1))/TSPRA)
      SUMR=SUMR+R
      DO 4 J=1,II
        4 AN(J)=AN(J)/TSPR
        TSPRA=1.-AN(1)
C.... THE FALL PROPORTION OF FAWNS (FFDR), REPRODUCTIVE PERFORMANCE
C.... (RPRE), SPRING RATE OF RECRUITMENT (SFDR), AND RATE OF INCREASE
C.... (R) ARE WRITTEN ON OUTPUT FILE 3.
      WRITE(3,300) FFDR,RPRE,SFDR,R
      3 CONTINUE
C.... THE MEAN EXPONENTIAL RATE OF INCREASE (SUMR) AND THE MEAN
C.... ANNUAL RATE OF INCREASE (ALAMDA) ARE CALCULATED.
      SUMR=SUMR/NYRS
      ALAMDA=EXP(SUMR)
      WRITE(6,202)SUMR,ALAMDA
      WRITE(6,203) DSEED
100  FORMAT(A1)
203  FORMAT(1H,"DSEED =",D21.10)
200  FORMAT(1H,"ENTER RANDOM NUMBER")
201  FORMAT(1H0,"PRINCIPLE EIGANVALUE =",F5.3)
202  FORMAT(1H,"MEAN R VALUE =",F6.3,3X,"MEAN LAMDA VALUE =",F6.3)
204  FORMAT(1H,"FALL PROPORTION TO BE ESTIMATED?--YES OR NO"/)
205  FORMAT(1H,"ENTER FALL SAMPLE SIZE"/)
206  FORMAT(1H,"WINTER SURVIVAL TO BE ESTIMATED?--YES OR NO"/)
207  FORMAT(1H,"ENTER WINTER SAMPLE SIZE"/)
300  FORMAT(4F10.6)
      STOP
      END
SUBROUTINE INPUT
C**** THIS SUBROUTINE READS IN THE INPUT PARAMETERS FOR THE POPULATION.
COMMON/AA1/II,SS(12),SW(12),FEC(12),AN(12),NYRS
COMMON/AA3/SSPC(12),SWPC(12),FECPC(12)
READ(2,100)II,NYRS
READ(2,101)(SS(I),I=1,II)
READ(2,101)(SW(I),I=1,II-1)
READ(2,101)(FEC(I),I=1,II)
READ(2,101)(SSPC(I),I=1,II)
READ(2,101)(SWPC(I),I=1,II-1)
READ(2,101)(FECPC(I),I=1,II)
100  FORMAT(I2,1X,I4)
101  FORMAT(12F6.0)
      RETURN
      END
SUBROUTINE STABLE(PEV)
C**** THIS SUBROUTINE CALCULATES THE INITIAL STABLE AGE DISTRIBUTION.
COMMON/AA1/II,SS(12),SW(12),FEC(12),AN(12)
COMMON/CC1/S(12),F(12)
AN(1)=1.
T=1.
DO 1 I=2,II
  AN(I)=AN(I-1)*S(I-1)/PEV
  1 T=T+AN(I)
DO 2 I=1,II
  2 AN(I)=AN(I)/T
      RETURN
      END

```

```

SUBROUTINE FALL(DSEED)
C**** THIS SUBROUTINE CALCULATES THE FALL POPULATION, ESTIMATED FALL
C**** PROPORTION OF FAWNS (FFDR), AND REPRODUCTIVE PERFORMANCE (RPRE).
COMMON/AA1/II,SS(12),SW(12),FEC(12),AN(12)
COMMON/AA2/SSM(12),SWM(12),FECM(12)
COMMON/BB1/TFALL,FFDR,TSPR,SFDR,NFALL,NWINT,RPRE,FAWN,IXX,IYY
DOUBLE PRECISION DSEED
C.... THIS SECTION CALCULATES THE FALL POPULATION IN EACH AGE CLASS
C.... (AN(I)), FALL PROPORTION OF FAWNS, AND REPRODUCTIVE PERFORMANCE.
TFALL=0.0
FAWN=FAWN*(SS(1)+SSM(1))
DO 1 I=1,II
AN(I)=AN(I)*(SS(I)+SSM(I))
1 TFALL=TFALL+AN(I)
FFDR=AN(1)*2./(AN(1)*2.+TFALL-AN(1))
RPRE=2.*FAWN/(TFALL-AN(1)-AN(2))
IF(IYY.EQ.1HN) GO TO 10
C.... THIS SECTION CALCULATES AN ESTIMATE OF THE FALL PROPORTION OF
C.... FAWNS (FFDR).
CALL RANNO(2,DSEED,RAN)
FF=FFDR*(1.-FFDR)/NFALL
FFDR=FFDR+SQRT(FF)*RAN
IF(FFDR.LT.0.0) FFDR=0.0
IF(FFDR.GT.1.0) FFDR=1.0
10 IF(IXX.EQ.1HN) RETURN
C.... THIS SECTION CALCULATES AN ESTIMATE OF THE OVERWINTER SURVIVAL
C RATE OF FAWNS (SF), THE OVERWINTER SURVIVAL RATE OF ALL FAWNS
C AND DOES (SA), AND THE ESTIMATED PROPORTION OF FAWNS IN THE
C.... SPRING POPULATION (FFDR).
TOTA=0.0
DO 3 I=3,II
3 TOTA=TOTA+AN(I)
TA=(TOTA-AN(II))*(SW(3)+SWM(3))
TJ=AN(2)*(SW(2)+SWM(2))
TF=AN(1)*2.*(SW(1)+SWM(1))
SAI=(TF+TJ+TA)/(AN(1)*2.+AN(2)+TOTA)
SA=SAI*(1.-SAI)/NWINT
CALL RANNO(2,DSEED,RAN)
SA=SQRT(SA)*RAN+SAI
IF(SA.LE.0.0) SA=.00001
IF(SA.GT.1.0) SA=1.0
CALL RANNO(2,DSEED,RAN)
SF=SW(1)+SWM(1)
SF=SF*(1.-SF)/NWINT
SF=SQRT(SF)*RAN+SW(1)+SWM(1)
IF(SF.LT.0.0) SF=0.0
IF(SF.GT.1.0) SF=1.0
FFDR=FFDR*SF/SA
RETURN
END

```

```

SUBROUTINE SPRING(DSEED)
C**** THIS SUBROUTINE CALCULATES THE TOTAL SPRING POPULATION
C (TSPR), THE NUMBER IN EACH AGE CLASS (AN(I)), AND THE SPRING
C**** RECRUITMENT RATE (SFDR).
COMMON/AA1/II,SS(12),SW(12),FEC(12),AN(12)
COMMON/AA2/SSM(12),SWM(12),FECM(12)
COMMON/BB1/TFALL,FFDR,TSPR,SFDR,NFALL,NWINT,RPRE,FAWN,IXX,IYY
DOUBLE PRECISION DSEED
TSPR=0.0
DO 1 I=1,II-1
J=II+1-I
AN(J)=AN(J-1)*(SW(J-1)+SWM(J-1))
1 TSPR=TSPR+AN(J)
SFDR=AN(2)/(TSPR-AN(2))*2.
AN(1)=0.0
DO 2 I=2,II
2 AN(1)=AN(1)+AN(I)*(FEC(I-1)+FECM(I-1))
FAWN=AN(1)-AN(2)*(FEC(1)+FECM(1))
TSPR=TSPR+AN(1)
RETURN
END
SUBROUTINE LIMITS(KKX,DSEED)
C**** THIS SUBROUTINE CALCULATES THE FECUNDITY AND SURVIVAL RATE
C**** MODIFIERS FOR EACH YEAR.
COMMON/AA1/II,SS(12),SW(12),FEC(12)
COMMON/AA2/SSM(12),SWM(12),FECM(12)
COMMON/AA3/SSPC(12),SWPC(12),FECPC(12)
DOUBLE PRECISION DSEED
CALL RANNO(KKX,DSEED,RAN)
DO 1 I=1,II
1 SSM(I)=SSPC(I)*RAN
CALL RANNO(KKX,DSEED,RAN)
DO 2 I=1,II-1
2 SWM(I)=SWPC(I)*RAN
CALL RANNO(KKX,DSEED,RAN)
DO 3 I=1,II
3 FECM(I)=FECPC(I)*RAN
RETURN
END
SUBROUTINE RANNO(KK,DSEED,RAN)
C**** THIS SUBROUTINE RANDOMLY SELECTS NUMBERS FROM A UNIFORM
C (KK=1) OR NORMAL (KK=2) DISTRIBUTION USING THE IMSL
C**** FUNCTIONS GGUBFS AND GGNQF.
DOUBLE PRECISION DSEED
IF(KK.NE.1) GO TO 10
RAN=GGUBFS(DSEED)
RAN=RAN*2.-1.
RETURN
10 RAN=GGNQF(DSEED)
RETURN
END

```

```

SUBROUTINE PREIG(II,PEV)
C**** THIS SUBROUTINE CALCULATES THE PRINCIPLE EIGANVALUE
C**** FOR A MATRIX.
COMMON/CC1/ S(12),F(12)
DIMENSION AI(12),A(12),ALL(12),C(12),AL(12),A1(12)
10 RO=0.
T=0.
B=0.
AI(1)=1.
DO 1 K=2, II
1 AI(K)=AI(K-1)*S(K-1)
DO 2 K=2, II
RO=RO+AI(K)*F(K)
T=T+K*AI(K)*F(K)
2 AL(K)=0.
T=T/RO
R=ALOG(RO)/T
DO 3 K=1, II
3 B=B+AI(K)*EXP(-R*K)
B=1./B
DO 8 K=1, II
8 A(K)=AI(K)*B*EXP(-R*K)
4 CONTINUE
AA=0.
AB=0.
SAL=0.
DO 5 K=1, II
AA=AA+A(K)
5 ALL(K)=AL(K)
DO 6 K=1, II
C(K)=A(K)/AA
A1(K)=F(K)*C(K)
AB=AB+A1(K)
IF(K.EQ.1) GO TO 6
A(K)=S(K-1)*C(K-1)
AL(K)=A(K)/C(K)
6 CONTINUE
A(1)=AB
AL(1)=A(1)/C(1)
DO 7 K=1, II
7 IF(ABS(ALL(K)-AL(K)).GE.,00001) GO TO 4
DO 9 K=1, II
9 SAL=SAL+AL(K)
PEV=SAL/II
RETURN
END

```

A sample 'run' of the program MULEDEER is shown below. User supplied input values are underlined.

R MULEDEER  
#RUNNING 2769

ENTER RANDOM NUMBER  
#?  
2564884.D0

FALL PROPORTION TO BE ESTIMATED?--YES OR NO  
YES

ENTER FALL SAMPLE SIZE  
200

WINTER SURVIVAL TO BE ESTIMATED?--YES OR NO  
NO

PRINCIPLE EIGANVALUE =1.000  
MEAN R VALUE =-0.007    MEAN LAMDA VALUE = 0.993  
DSEED =            .1213320329D+10

A sample of the output file 3 is shown below for a 30-year simulation of the model used to test hypotheses H2 and H3. Each line represents one year. The four columns are the estimated proportion of fawns in the fall population (FFDR), the reproductive performance of the population (RPRE), the spring rate of recruitment (SFDR) and the rate of increase of the population (R), respectively.

FFDR	RPRE	SFDR	R
0.381092	0.679862	0.502335	-0.098190
0.526265	1.592467	0.938469	0.151735
0.422419	1.231140	0.421775	-0.244335
0.400126	0.573758	0.388506	-0.200872
0.581298	1.387663	0.967034	0.138526
0.362066	0.724949	0.479395	-0.105183
0.398526	0.608338	0.426111	-0.090019
0.499916	1.182167	0.763314	0.092093
0.406159	1.359455	0.477199	-0.185499
0.592617	1.487186	0.894092	0.068969
0.347671	0.611095	0.307204	-0.202405
0.520254	1.295909	0.821588	0.025542
0.404461	0.801498	0.428250	-0.189678
0.427944	0.631728	0.590125	-0.002339
0.544471	1.289785	0.725035	0.035825
0.497355	1.532164	0.899305	0.061899
0.535375	1.461479	0.905715	0.153426
0.286584	0.646067	0.360160	-0.117582
0.408305	0.640282	0.454457	-0.099641
0.384024	0.847455	0.503754	-0.059929
0.452720	0.957359	0.681155	-0.006834
0.554760	1.910325	0.900842	0.101857
0.286338	0.571469	0.386421	-0.133048
0.511775	1.723276	1.122691	0.238521
0.513423	2.034278	0.905637	0.135669
0.448255	1.548213	0.818998	0.051099
0.498579	1.529238	0.724900	0.006216
0.383499	0.909284	0.420956	-0.203193
0.442431	0.876769	0.593980	-0.051484
0.325141	0.614321	0.362443	-0.156731