THESIS

SIMULATION MODELING OF BIG GAME AT

WICHITA MOUNTAINS WILDLIFE REFUGE

Submitted by

Gary L. Williams

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University
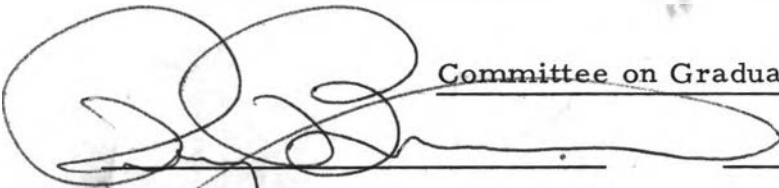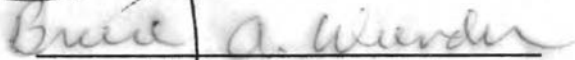
Fort Collins, Colorado

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED

UNDER OUR SUPERVISION BY GARY L. WILLIAMS ENTITLED

SIMULATION MODELING OF BIG GAME AT WICHITA MOUNTAINS

WILDLIFE REFUGE BE ACCEPTED AS FULFILLING IN PART

REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

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Adviser

ABSTRACT OF THESIS

SIMULATION MODELING OF BIG GAME AT

WICHITA MOUNTAINS WILDLIFE REFUGE

Certain aspects of the population ecology of herds of bison

(Bison bison), elk (Cervus canadensis), white-tailed deer

(Odocoileus virginianus), and Texas longhorn cattle (Bos taurus)

inhabiting the Wichita Mountains Wildlife Refuge in southwestern

Oklahoma were investigated by analyzing data contained in existing

refuge reports and related documents. The information obtained was

subsequently used in validation studies for a simulation model

(Program ONEPOP) designed to mimic the dynamics of big game

grazing systems.

The factors which influenced population sizes most in the four

populations were harvest rate of the previous year and reproductive

rate. In all four populations, natural mortality rates tended to be

density independent whereas reproductive rates were density depen-

dent. Ecological factors which influenced herd reproductive rates

were precipitation amount and food supply. The amount of precipita-

tion received during August and September, immediately prior to and

during the breeding period, may have had greater influence on re-

productive rates than total annual precipitation. Incidence of

pregnancy among yearling females was especially high during years of above-average precipitation. There was also evidence that lactation status affected reproductive rates in elk. In general, there was an inverse relation between lactation and pregnancy among Wichita elk.

Computer simulations with Program ONEPOP closely mimicked reported values for population size and trend, reproductive parameters, harvest, and sex and age structures in the bison and longhorn cattle populations. Simulated population sizes for elk, however, were substantially higher than corresponding reported values and led to the conclusion that the Wichita elk population had been underestimated for several years. Demographic data for white-tailed deer were too poor to adequately test the model.

Results indicated that Program ONEPOP simulated big game population dynamics with a high degree of precision and realism. The model contained the basic parameters which produced population changes over time and was consistent with population controlling mechanisms. The model appeared to have the capability of generating information useful in herd management.

Gary L. Williams
Fishery and Wildlife Biology
    Department
Colorado State University
Fort Collins, Colorado 80523
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INTRODUCTION

Wildlife management as a profession has gone through at least two important phases during the course of its development. Hickey (1974) described an "awareness phase" which occurred in the United States during the late 1800's. It was during this era that naturalists voiced concern about species reductions, over-exploitation and habitat destruction. Their actions created alarm among the citizenry and eventually gave rise to the wildlife conservation movement in the United States.

During the 1930's, Aldo Leopold introduced what might be termed the "scientific phase" of wildlife management. He established the concept that habitat conditions are the basis for effective game management. Thus, Leopold's work (1933) called attention to the need for considering habitat and population components not as individual entities but as elements of an interactive system. Leopold also defined the goal of sustained annual yield towards which the system should work. To the extent discussed above, Leopold's ideas represented a "systems" approach (Churchman 1968) to wildlife management.

It seems likely that wildlife management would benefit by becoming move systems orientated in the future. Basically the benefits which would accrue to wildlife management from adopting the systems

approach fall into two broad categories. First the development of computer models, a fundamental aid in the application of the systems approach, could assist in the advancement of knowledge by guiding field experimentation in a method Holling (1966) referred to as experimental components analysis.

Aside from providing direction for field studies, computer models, once developed and tested, could make equally important contributions to the decision-making aspects of wildlife management. Computer models could be used to play "what if" games to test alternative management strategies and elucidate their most-probable consequences without lengthy delays or damage to the field resource. From such a vantage point, the decision-maker might be more proficient in designing management programs best suited to the myriad biological, political and social constraints under which he must function.

Pursuant to these beliefs, a research project (of which the current study was a part) was undertaken whose basic objective was the development of a simulation model which could be used by decision-makers involved with big game resources. Development of the model preceded the undertaking of the present study and benefited from the input of individuals from both academic and applied-management concerns.

To achieve maximum flexibility and utility, the model was developed around explicit guidelines. For example, to provide the broadest possible use, the model was developed without reference to any particular set of data, geographic locale or species of big game. The capability of the model to closely duplicate the real world was assured by designing a dynamic, deterministic program which would mimic essential interactions between population and habitat components. The structure and function of the computer model (Program ONEPOP) is reviewed in the METHODS section of this paper and was discussed in detail by Gross et al. (1973).

The Problem

Once a model has been formulated, its ability to reproduce the characteristics and behavior of the real-world system must be tested. A model can be useful only to the extent that it enhances our ability to represent reality. Therefore, a critical step in the development of any model is measuring the model's ability to replicate the performance of its real-world counterpart within acceptable limits. Testing the model for goodness of fit with the real-world system is often referred to as "model validation" (Lee 1973) and it is in this respect that the findings presented herein relate to the overall research project mentioned above.

The present study represented one of three similar studies conducted on national wildlife refuges in the western United States undertaken to field test or validate Program ONEPOP. The specific assignment was to: (1) investigate the population biology of four big game populations inhabiting the Wichita Mountains Wildlife Refuge, (2) determine the extent to which Program ONEPOP mimicked the essential interactions between those populations and their habitat components and, (3) determine Program ONEPOP's compatibility with population controlling mechanisms operating within the populations.

<div align="center">Approach to the Problem</div>

By definition, validation deals with ascertaining a model's ability to reproduce the real-world system. But that task is complicated by at least two important facts. First, there are few real-world systems about which we have <u>perfect</u> information. This is especially true of big game grazing systems where we may have very good information about some system parameters as annual harvest or reproductive rates but lack information about other system parameters as population density or natural mortality. Thus, even if the model were an exact duplicate of the real-world system, we could seldom demonstrate that fact because of real-world data limitations.

The second important fact which complicates the task of model validation is that models obviously can never duplicate the real-world system in every respect. Models are simplified and generalized statements of what seem to be the most important characteristics of the real-world system (Lee 1973). It is therefore impossible for a model to exactly mimic the real-world system as a consequence of its simplified formulation.

These two properties of real-world data bases and model structure make the task of model validation extremely difficult. In fact, some authors (Forrester 1961; Lee 1973) have suggested that a model can never be "proved," at least in the rigorous mathematical sense. It may be that the only realistic way of showing a model to be valid is to compare it with alternative ways of representing the system. If the model allows us to better understand system complexity and dynamics than alternative representations do, then we should conclude that the model is valid.

In the absence of rigorous methods for proving the validity of simulation models, it becomes important to have a general framework in mind with which to test the model's validity. Holling (1966) has developed one of the few frameworks for judging the validity of simulation models. His approach consists of four validation criteria -- generality, resolution, precision and realism -- which provide a comparative framework to help organize the complexity of validation.

The validation criteria of generality and wholeness were not entirely consistent with the objectives of the Wichita study and therefore have been deleted. But Program ONEPOP has been discussed in terms of those two validation criteria by Gross et al (1973).

Holling's validation criteria of precision and realism were most consistent with the objectives of the Wichita study. These criteria are defined and the techniques used to assess them in terms of Program ONEPOP are discussed in the METHODS section. In general, the precision of Program ONEPOP was tested through its ability to produce simulated values which closely matched reported values whereas the model's realism was evaluated primarily in terms of its compatibility with population-controlling mechanisms and its assumed relations between demographic parameters.

DESCRIPTION OF STUDY AREA

The information upon which this study is based was gathered on the Wichita Mountains Wildlife Refuge. The nature of the research required that a minimal amount of time be actually spent on the refuge each year. Consequently no attempt was made to collect descriptive information about the area other than what has been previously published. The following description of the area has been summarized from various workers, especially Allred (1955), Buck (1964), Crockett (1964) and Halloran (1964).

Location and Administrative History

The Wichita Mountains Wildlife Refuge is a 23885-ha (59020-acre) expanse located in Comanche County, southwestern Oklahoma (Fig. 1). It is located approximately 24 km (15 miles) northwest of Lawton, Oklahoma and is contiguous on its southern boundary with Fort Sill Military Reservation. Private ranches adjoin the other refuge boundaries.

The area passed into public ownership in 1905 when the land, formerly part of the Apache-Kiowa-Comanche Indian Reservation, was converted to a national game preserve by presidential action. Initially the area was administered by the U.S. Forest Service and was known as the Wichita National Forest. In 1935, administrative

Oklahoma City

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Wichita Mountains
Wildlife Refuge

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Lawton
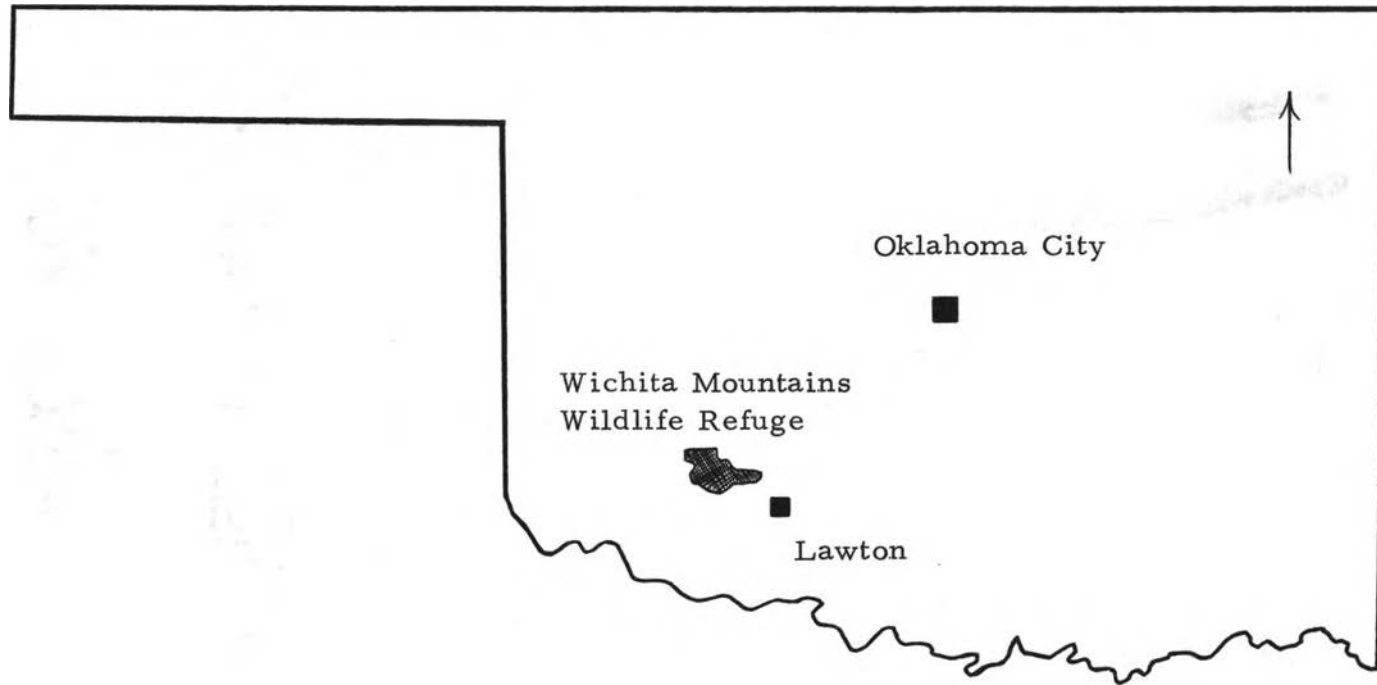
Figure 1.   Location of the Wichita Mountains Wildlife Refuge within the state of Oklahoma.

responsibility was transferred to the Biological Survey of the U.S. Department of Agriculture. Currently the area is administered by the Fish and Wildlife Service of the U.S. Department of Interior.

Climate

Climatic conditions on the refuge are of the continental type with temperature extremes of -26 C (-16 F) and 45 C (112 F) having been recorded. In general, winters are mild and dry whereas summers tend to be hot and humid. January has the coldest average temperate of 4 C (40 F) whereas July and August are the hottest months with an average temperate of 34 C (94 F).

Halloran (1964) reported an average of 77.2 cm (30.4 in) of moisture annually between 1906 and 1955. Of that total, approximately 75 percent occurred as rainfall between April and October. May is typically the wettest month of the year with an average rainfall of 10.9 cm (4.3 in) while January is often the driest month.

Birds and Mammals

The official species checklist for the refuge shows more than 200 species of birds and at least 50 species of mammals. A list of the common species is given in Appendix A.

Range Description

Blair and Hubbell (1938) pointed out that the Wichita Mountains Biotic District lies within the southern part of the Mixed Grass Plains District. Accordingly, the Wichita rangelands contain short-grass, mixed-grass and tall-grass prairies as well as woody-plant communities.

Grasslands

Grasslands prevail over most of the refuge. Crockett (1964) found the most common species to be little bluestem (Andropogon scoparius), big bluestem (A. gerardi), hairy gramma (Bouteloua hirsuta) and blue gramma (B. gracilis). Big bluestem and little bluestem tend to dominate areas having deep soils while hairy gramma dominates the shallow soils of open ridges.

Woody Plants

The most common forest association on the refuge is post oak (Quercus stellata) and blackjack oak (Q. marilandica). Along streams, valleys and other mesic areas, this association is displaced by stands of Shumard's oak (Q. shumardii), chinquapin oak (Q. muhlenbergii), American elm (Ulmus americana), walnut (Juglans rupestris), chittamwood (Bumelia lanuginosa) and sugar maple (Acer saccharum).

Land Use

Since the refuge was declared a national game preserve, herds of bison (Bison bison), Texas longhorn cattle (Bos taurus), elk (Cervus canadensis) and white-tailed deer (Odocoileus virginianus) have been maintained in the area. In addition, domestic animals (horses and cattle) were grazed on the Wichita ranges until the late 1930's. Ostensibly, domestic and wild ungulates did not graze in the same pastures. Prior to the late 1930's, the only fenced area on the refuge was a centrally-located pasture of about 3250 ha (8000 ac) referred to as the "Buffalo Pasture." The refuge's populations of bison, longhorn cattle and elk were kept within that area while domestic animals were permitted to graze the outlying areas.

Fencing of the entire refuge was completed in 1938 and, at that point, the Buffalo Pasture was dismantled and the wild herds were released onto the rangelands previously grazed by domestic animals. It seems likely that the wild herds were released onto over-grazed ranges. Halloran (1961) quoted Ira Gabrielson who observed in 1937 that cattle had depleted most of the range grasses and were feeding on oak leaves. Discussion presented in a later section describes the significance of that over-grazing in terms of demography of the wild herds.

METHODS

All of the data used in the present study were obtained from
existing records and publications. No additional field studies were
undertaken. Much of the information used came directly from
quarterly and/or annual reports prepared by the refuge staff and
submitted to the regional office. These reports were best described
as narrative summaries of the events and activities which occurred
on the refuge during the time period covered by the report and
typically contained information on range conditions, herd numbers
and disposals as well as mention of other items such as predation,
poaching and the incidence of disease in the herds.

In addition to the narrative summaries, the refuge files also
contained numerous special reports prepared since the early 1950's
which covered a variety of topics and more-or-less supplemented the
annual narratives. The special reports most beneficial to the
present research undertaking were those which reported findings of
census efforts, butcher records, and calving rates.

Information sources other than actual refuge reports were also
used. For example, the Oklahoma Department of Wildlife Conserva-
tion conducted an ecological investigation of the Comanche County
deer population between 1965 and 1968. Reports prepared during the
course of that investigation provided valuable supplemental

information. And, although not used directly in the present study, a third source of information was that gathered on the white-tailed deer population on Fort Sill Military Reservation. The Fort Sill information, mostly accounts of herd size, fawning rates and harvest summaries, was used as a cross-check of information reported for the Wichita refuge. For example, it was possible to cross-check fawning rates in the two areas during any given year since habitat conditions were somewhat similar.

Generally speaking, the quality of population information covering years prior to the early 1940's was poor. This was the period during which administrative responsibility for the area was shifted between agencies and reporting procedures were not consistent. Information sources for years subsequent to the 1940's, however, were generally good to excellent. There were instances where a particular datum was not collected (or reported) consistently over the years. That was most true of information about natural mortality and reproductive rates and least true of information about population sizes and removals. Another inconsistency in the data base was that the methods used to obtain information changed over time. To illustrate, during the 1960's, the policy was to assume a constant calving rate for the Wichita elk herd. Currently, however, elk calving rates are derived from cow:calf counts made in late summer and also from pregnancy-lactation data gathered on cows shot during the fall hunting season.

The quality of data bases varied greatly between the four ungulate species. As might be expected, demographic information was best for bison and longhorn cattle and poorest for elk and white-tailed deer. Additional comments regarding data quantity and quality are made in the section dealing with the synthesis of field data for each species.

Methods Used to Gather and Process Demographic Data

With few exceptions, the demographic data used to carry out the present study were obtained from photocopies made of refuge records and reports. Once copied, the records were searched and relevant information compiled into tables and charts.

In order to execute the simulation model, some of the data taken from the records had to be converted to another form. The most common data transformation was the conversion of reproductive data to linear regression functions which depicted how reproduction by the herd changed as herd size increased or decreased. Some percentages were also calculated for use in the simulation model.

Nature of the Population Model

Program ONEPOP, the basic computer model used in the study, has been presented in detail elsewhere (Gross et al 1973). Consequently only the basic nature of the model and the philosophy of its use are reviewed here.

Reduced to its most fundamental elements, Program ONEPOP integrated three population processes: reproduction, natural mortality, and harvest. Reproductive information was input to the program according to age class and was processed internally by the model in a variety of ways. The most commonly used method of simulating herd reproductive dynamics was with density-dependent (i.e. linear regression) functions. However, in addition to density-dependent functions, reproduction by the Wichita herds was simulated at times by specifying the exact number of young to be added to the herd.

Natural mortality rates were input to the model according to sex and age classification as well as the time of year during which the mortality occurred. Without exception, mortality information for the current study was input as a crude percentage of the age class lost during the mortality period being simulated.

Harvest information was likewise input to the program according to sex and age classification. While simulating the Wichita herds, the total number of males and females harvested annually was input and then partitioned by the model over the age classes to closely approximate the reported age structure of the harvest.

Immigration and emigration were not specifically considered in Program ONEPOP. The program assumed that the population being simulated represented a "closed system" i.e. that changes in herd

size and/or structure occurred only through changes in reproduction, natural mortality and/or harvest. Since the Wichita refuge was encircled by 8-foot fencing, that assumption appeared valid. It was necessary, however, to make special modifications in the program to account for the infrequent additions to the herds following their establishment on the refuge.

The simulation model operated on a 1-year time schedule with the beginning of the simulation year set at the time when young were born (essentially 1 June). The simulation year was divided into "mortality periods" of various duration which represented the time-keeping scheme in the model. For the Wichita simulations, the simulation year was divided into three mortality periods -- summer mortality, winter mortality and natural mortality occurring con-currently with the hunting season (disposal periods for bison and longhorn cattle).

Use of the Population Model

Data Analysis

Aside from the mechanical aspects of model operation and data input discussed above, a more-or-less standard procedure was followed to generate each herd simulation. The procedure involved simulating as many years of herd history as possible by employing processes referred to as "data alignment" and "data analysis."

Once the demographic data had been summarized and tabulated as discussed above, they were input into Program ONEPOP and became the basis for the first attempt to simulate the history of the herd. Judgment as to whether or not the simulation model was realistically simulating the history of the herd had to be made on the basis of subjective comparisons between simulated output and reported data (i.e. the alignment between corresponding population parameters was inspected). The population components checked for alignment typically included herd size and trend, herd sex and age structure, harvest, and reproductive rate.

Frequently, however, it was found that output generated by the simulation model did not agree with what had been collected in the field. Such discrepancies typically involved population sizes, reproductive rates, and natural mortality rates. The position taken in cases where the simulation model failed to satisfactorily replicate field data was that either the model was executing improperly or that the field data were in error.

Since Program ONEPOP was nothing more than an elaborate "bookkeeping system" which added and subtracted animals according to prescribed rules, the mathematical logic of the program was easily verified by hand calculations. Much more perplexing were those instances in which the simulation model was found to be executing correctly and an apparent error in the field data had been

uncovered. When inaccurate field data were detected, it was possible to continue with the simulation only after approximating more-nearly correct values for the erroneous (or missing) field data through an "alignment process" described as follows.

Data Alignment

Perhaps the most effective way of explaining how erroneous and/or missing field data were approximated is by means of analogy. Consider an individual who is assembling a jigsaw puzzle. If that individual has access to all pieces of the puzzle and all of those pieces are of the correct shape and size to interlock with other pieces, he should be able to assemble the puzzle without much diffi- culty. At first, the assembler would have to rely upon intuition or previous knowledge to position the puzzle pieces. But as more-and- more pieces are correctly fitted into position, finding the pieces which interlock with those already in position becomes easier.

Simulation of herd histories with Program ONEPOP was similar to the jigsaw-puzzle analogy in several respects. First, the pieces of the jigsaw puzzle are synonymous with the pieces of field data used in the simulation. A second simularity involves the goals of the respective activities. Whereas the goal of assembling a jigsaw puzzle is to fit together the numerous pieces to create a picture or other design, the goal of the simulation effort was to fit together

numerous pieces of demographic field data to recreate the "picture"

of herd dynamics reported over time.

In much the same way an individual assembling a jigsaw puzzle

relies upon intuition or previous knowledge to guide his actions,

efforts to approximate missing or incorrect field data were "guided"

by the best field information available. All reported data required

for the simulation were first ranked according to their "reliability";

the data were then input into the simulation, and lastly, if reported

and simulated values did not agree, the pieces of data known with

least accuracy were adjusted so as to best interlock with accurately-

known data.

Checking the Population Model for Precision and Realism

Precision has been defined by Gross et al (1973) as a validation

criterion concerned with the ability of a simulation model to generate

over a period of time values for parameters contained within the

model which approximate real-world values. From that definition,

model precision appears to be an attribute which can be quantified

through routine statistical procedures. Draper and Smith (1966)

pointed out that the amount of association between variables may be

ascertained by computing the degree of statistical correlation

between them. It therefore seemed appropriate to determine the

precision of Program ONEPOP by computing the amount of statistical

correlation (r^2 value) between its simulated output and corresponding reported information. The population parameters for which precision checks were made represented the "essential features" of big-game grazing system and included parameters as reproduction, harvest, population size, and population trend.

Gross et al (1973:60) also defined the validation criterion of realism as a "learning criterion that is related to the ability of the model to provide insight into the behavior of the essential features when they function as a system." If it seemed logical that the precision of Program ONEPOP could be tested with statistical procedures, it was equally apparent that statistical tests were largely inappropriate for ascertaining the model's realism.

There are no statistical procedures which allow an investigator to (1) determine whether or not several independently collected pieces of data (as population size, harvest rate, and natality rate) complement one another and to also (2) ascertain the extent to which those data function in unison as a logical system. Because of the inappropriateness of statistical procedures, it was necessary to test the realism of Program ONEPOP in a more-or-less intuitive manner.

An implication of the definition of realism given above is that a simulation model would exhibit realism if it demonstrated conclusively that the values of one or more measured components of the system being simulated were inconsistent with the values of other

measured components. It was in this manner that Program ONEPOP

demonstrated realism during the Wichita study. At various times,

the program demonstrated that the real-world population could not

have attained reported levels and trend if natality rates, total annual

harvest, and natural mortality losses were in fact as reported. Thus,

Program ONEPOP exhibited realism by demonstrating the mathe-

matical impossibility of certain reported data combinations.

POPULATION BIOLOGY AND DATA SYNTHESIS

The objective of this section is to provide a summary of the demographic biology of each big game species on the Wichita refuge and describe how field data were synthesized prior to computer simulation. In some instances, comparisons have been drawn between data for the Wichita herds and herds elsewhere in the United States. The information presented also provides the basis for later discussions dealing with demographic mechanisms operating within the populations.

Bison Field Data

Bison were established in the Wichita Mountains through the cooperative efforts of the New York Zoological Society and the American Bison Society. During October 1907, 15 bison (7 bulls and 8 cows) were transferred from the New York Zoological Park and released onto the Wichita National Forest in an effort to perpetuate the species and prevent its extinction. No longer threatened by extinction, bison are currently maintained on the refuge mostly for public viewing. Surplus animals are disposed of each year, but management places more emphasis on maintaining a show herd and less on managing for maximum production.

In many ways, the management of bison on the Wichita is similar to that practiced on carefully-managed cattle ranches. The animals are rounded up each fall at which time herd counts and classifications are made, the animals to be disposed of are selected and, until recently, female calves were vaccinated for brucellosis (Brucella abortus). Bison are free-ranging on the Wichita and receive no dietary supplements other than salt.

Reproduction

A considerable amount of effort is expended by the refuge staff each fall collecting information about the reproductive performance of the herd. During the fall roundup, calves are counted and sexed, a calf:cow ratio is determined and a total count of the herd is made. To supplement this information, there have been special studies undertaken during the past to ascertain the frequency with which bison cows on the Wichita produce calves. More will be presented on this topic below.

Breeding Age. Bison cows on the Wichita typically first breed as 2-year-olds. Halloran (1967) reported that 26 of 35 (74 percent) cows 3 years old had produced calves and therefore had bred when 2 years old. Bison on the Wichita have bred at 12 to 15 months of age and produced calves as 2-year-olds (Halloran 1960) but this appears to be a rare occurrence. These findings for the Wichita agree with results reported in other studies. Haugen (1974) found

only 1 of 17 1½-year-old cows which had ovulated in his study of bison in South Dakota and Nebraska and she was not pregnant. However, he also found 34 of 39 (87 percent) cows 2½ years old from the same areas which were pregnant. Likewise Barney and Cunningham (1970) stated that they had observed no cows on the Theodore Roosevelt National Memorial Park giving birth at 2 years of age and, consequently, based all of their estimates of reproduction on cows 3 years old and older.

The age at which bulls attain sexual maturity has not been established on the Wichita but notes prepared on the herd in 1928 mentioned bulls breeding as 2-year-olds. Haugen's (1974) study of bison bulls revealed that they actively produce sperm as yearlings. But he speculated that yearling bulls would lack the social dominance necessary to assume a very active role during the rut.

Halloran and Glass (1959) stated that rutting activity among bison on the Wichita occurred in June and July with the calves being born in late March and early April. This was earlier than the dates derived by Haugen (1974) from his aging of bison embryos. Haugen estimated bison in South Dakota and Nebraska conceive between late July and mid-August with the peak occurring about 1 August.

Calving Rate Comparisons and Trend. Calving rates for bison in the Wichita Mountains appear to be lower than those reported from other areas. The average calving rate for bison on the Wichita

between 1960 and 1967 was 52 calves per 100 cows based upon animals 2 years old and older. After this period, calf crop percentages have been based upon cows 3 years of age and older and, therefore, must be excluded from the average. By way of comparison, Haugen (1974) reported finding 121 of 160 (76 percent) cows pregnant which would have been at least 2 years old at calving time. Assuming low prenatal mortality, Haugen's data suggest a calf crop approaching 80 calves per 100 cows. Roelle (1971) also reported calving rates for bison on the National Bison Range approaching 80 calves per 100 cows.

The reasons for lower calving rates on the Wichita than other areas are not known but evidence suggests that the condition has not always existed. Roelle (1971) compared reproductive rates for bison on the Wichita with those from the National Bison Range. His analysis revealed that, at the time of introduction (about 1910), bison reproductive rates on the Wichita were considerably higher than those on the Bison Range. The situation reversed itself, however, as the herds increased on both areas such that currently reproductive rates on the Bison Range are substantially higher than those on the Wichita.

These comparisons in bison reproductive rates may be an indication of habitat conditions on the respective areas. It seems conceivable that the higher reproductive rates observed for bison on the Bison Range and the areas surveyed by Haugen might be due in

part to better range conditions in those areas than what occurred on the Wichita.

Calving rates for bison declined during the first 15 years of their residence on the Wichita (Fig. 2). This period of reproductive decline was followed by a period during which calving rates were relatively constant but bison calving rates increased from the late 1930's to about 1960. In addition, bison calving rates reported after 1960 were slightly higher than those reported prior to 1960 but those increases are believed due to the manner in which the rates were calculated.

The reasons for an increase in bison calving rates are unknown but perhaps husbandry actions taken during the late 1930's and early 1940's were contributing factors. Vaccination of bison for brucellosis began in 1941 and no doubt improved reproductive success of the herd. Brucellosis is reported to have occurred among bison on the Wichita refuge during the early 1940's according to Bartnicki (1972). Two other actions which perhaps brought about an improvement in bison reproductive performance were the effect of lowered stocking rates following modification of the Buffalo Pasture plus the impact of the gradual improvement in range condition following the termination of grazing leases in 1938.

Fluctuations in Bison Natality. A brief examination of Fig. 2 is sufficient to demonstrate that natality rates for bison on the Wichita
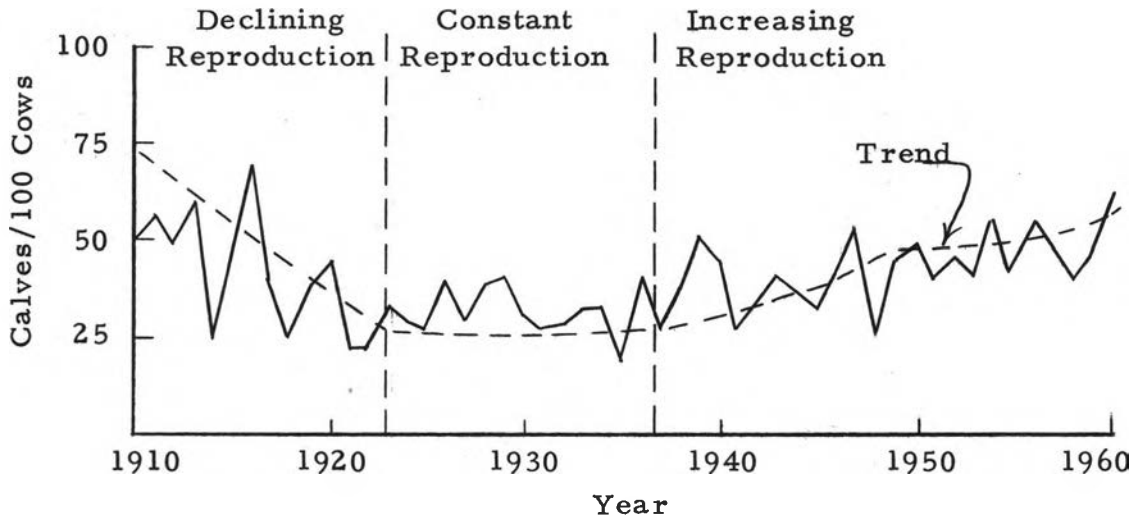
Figure 2. Long-term trend in bison reproductive rates on the Wichita
          Mountains Wildlife Refuge. Rates are based upon the total
          number of females in the herd at time of calving.

refuge have not been consistent from year to year. The biological causes of such fluctuations are not known but part of the variation may have been caused by cows giving birth every second year rather than consecutive years.

A study designed and carried out by members of the refuge staff (Halloran 1967) suggested that bison cows on the Wichita tend to give birth in alternating years. In that study, the reproductive status of 50 marked cows was observed and recorded over a 9-year period. Results, summarized in Table 1, revealed that cows of this group produced their first calf at 2 years of age and that calf crop percentages were higher in alternating years. The results of the study would be consistent with a pattern in which a majority of the cows under observation gave birth in alternating years.

If many of the bison cows on the Wichita do in fact produce calves in alternating years, it might provide additional evidence that habitat conditions on the Wichita are poor for bison. As pointed out above, calving rates among bison on the National Bison Range and in areas of Nebraska and South Dakota approach 80 calves per 100 cows annually. To achieve calf crops of that magnitude on a consistent basis, a large portion of the cows must bear a calf each year. Again, the calving pattern observed on the Wichita could signal range conditions that are too poor to supply the necessary nutrition for cows to bear a calf each year or the stocking level (about 800 head when the

Table 1. Nine-year calving record of 50 bison cows marked as
calves on the Wichita Mountains Wildlife Refuge (data from
Halloran 1967).

Age (Years)	Number of Cows Observed	Number of Calves Seen	Percent Calf Crop
1	--	--	--
2	--	--	--
3	35	26	74.3
4	34	17	50.0
5	30	22	73.3
6	34	19	55.9
7	33	28	84.8
8	32	20	62.8
9	21	12	57.1

calving study was completed) may have been too high to permit adequate nutrition for each cow in the herd.

Synthesis of Bison Reproductive Functions. Causal mechanisms aside, the variation in bison calving rates over time made it impossible to synthesize density-dependent reproductive function for the herd, at least for all but the first few years bison occupied the refuge. Synthesis of density-dependent functions was impossible because when reported calving rates were plotted against population sizes, the data points were scattered about the calculated regression to the extent that the regression was an imprecise description of reported calving rates; the calculated regression fitted the reported values for calves per cow so poorly that when the synthesized rate was used in the simulator, the simulated calf crops were invariably much above or below the corresponding real value. In order to simulate bison reproduction, the following non-regression approach had to be employed.

Field records for the total number of calves born each year on the Wichita appeared to be complete and accurate. Therefore, historical bison simulations were based upon actual reported calf totals for those years during which bison calving rates were too erratic to permit the synthesis of accurate density-dependent reproductive functions. The number of calves born into the simulated population equaled the yearly totals reported by Halloran (1964)

through the early 1960's and the number of calves cited in annual reports for subsequent years. In compliance with information reported by Halloran (1956), male and female calves were assumed to be recruited equally into the simulated population.

Natural Mortality

Natural losses in the Wichita bison herd have been low, with the deaths generally equal to less than 6 percent of the herd total. The exception occurred during the 1930's when reported loss in at least one instance exceeded 15 percent of the herd total (Fig. 3).

Causes of the natural losses have not usually been identified. Deaths caused by scours were a major problem during the 1930's but this source of mortality seems to have posed few problems in more recent years. Likewise little information has been recorded on the sex and age of bison dying from natural causes. Halloran (1956) reported that of the 391 bison deaths between 1908 and 1954 attributed to accidents and other natural causes, 168 (43 percent) were bulls while 223 (57 percent) were cows. These data do not necessarily reflect a higher incidence of mortality among cows than bulls. The greater number of female deaths may simply be an artifact of the higher percentage of cows than bulls in the herd during that period (Anonymous 1927).

The initial simulations for bison assumed an average herd mortality rate of 6 percent annually. But the rate was adjusted from
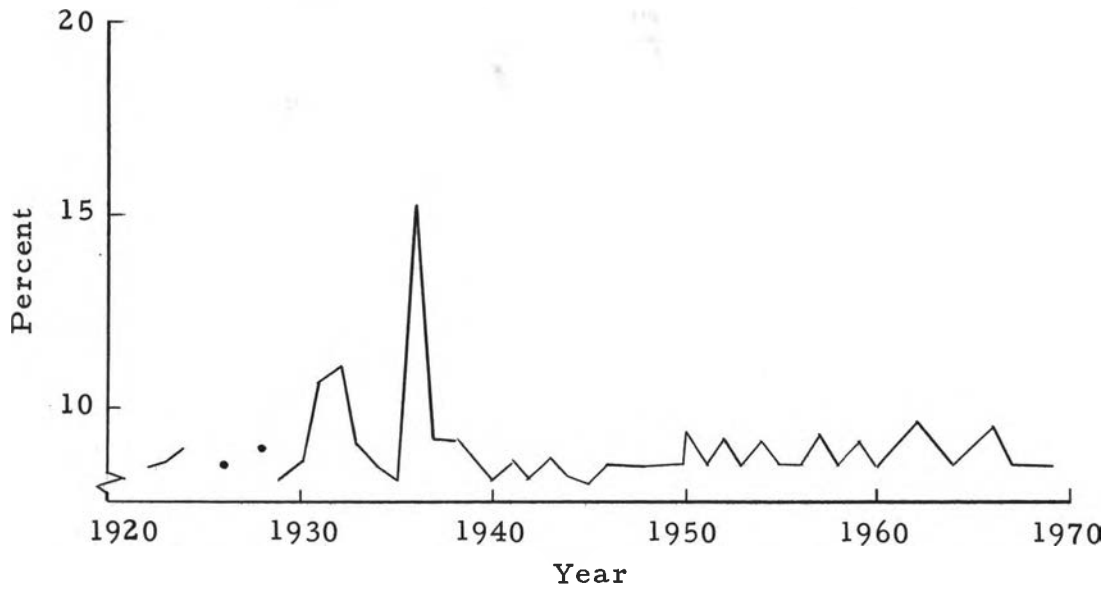
Figure 3. Magnitude of natural losses in the bison herd on the Wichita Mountains Wildlife Refuge. Percentages are based upon estimates of population size immediately after calving.

time-to-time so as to align reported and simulated population size and trend. In addition, sex-specific natural mortality information was among the poorest pieces of field data available for the bison population. Therefore, natural losses in the simulated population were applied equally to both sexes.

Information on Bison Removals

The number of bison removed from the herd each year as reported by Halloran (1964) and harvest totals taken from narrative reports for later years served as harvest information in the bison simulations. The initial assumption was that bison were removed from each age class relative to the size of that age class in the population. But harvest rates were adjusted from time-to-time to best align age structures in much the same manner as sex structure of the harvest was adjusted to align reported and simulated values for herd sex ratio.

Longhorn Cattle Field Data

The Texas longhorn figured prominently in the settling of the American western frontier. The breed was at its peak in the 1880's but, by the turn of the century, it was threatened by extinction as a result of cross-breeding between the longhorn and other introduced breeds. The breed might well have become extinct had it not been for the 30 head (20 cows, 3 bulls, 3 steers, and 4 calves) which were

collected from ranges in Texas and brought to the Wichita refuge in 1927 in a conservation move aimed at preserving the breed in its ancestral form. The present Wichita herd as well as the herd at Fort Niobrara National Wildlife Refuge has descended from these 30 animals plus a few additional animals added for breeding purposes (Halloran 1964).

Halloran and Shrader (1960) described the general management techniques and policies for longhorn cattle on the Wichita. Although longhorn cattle might be considered by some individuals to be domesticated, they are managed in much the same manner as the other big game herds on the refuge. They are granted relatively-free access to the entire refuge throughout most of the year and, over time, have developed behavior towards man typical of other forms of wildlife.

Basically the management of longhorn cattle on the refuge parallels that described above for bison. The animals graze over much of the refuge rangeland and receive no dietary supplements other than salt. Current refuge policy limits the herd to 300. The herd increased rapidly after its introduction in 1927, attaining the 300-head restriction by the early 1950's. Thus, for the past 25 years, herd level has essentially been held constant by removing a number of animals from the herd approximately equal to the annual calf crop. Surplus animals are sold through public auction or donated to zoos and other organizations.

During fall, the animals are rounded up by riders on horseback. At that time, all calves are branded and, until recently, all female calves were vaccinated for brucellosis. Animals being considered for disposal are tested for brucellosis and tuberculosis. Record sheets are also prepared for each animal which contains information on brand number, color pattern, sex, year of birth and lineage.

Reproductive Biology

Selective Breeding. The mission of longhorn management on the refuge is to preserve species characteristics. To facilitate that objective, breeding of longhorn cows is carefully controlled. Bulls having desired traits are selected for breeding and are placed in pastures with cows, often in mid-May and remain until mid-August. Calves are born between March 1 and June 15 (Halloran 1956a).

The selective breeding program being practiced on the Wichita could lead to an undesired condition by reducing the amount of genetic diversity within the herd. To circumvent the problem, new breeding stock is introduced at frequent intervals. A summary of introductions through the early 1970's is presented in Table 2.

Breeding Age. Longhorn females have attained sexual maturity by 1 year of age and are capable of giving birth during their second year of life. The refuge's data are confusing regarding the age at which cows are first bred but it appears that, prior to 1957, females were bred as yearlings. After that date, it seems to have been

Table 2. Number of bulls and cows added to the Wichita Mountains
Wildlife Refuge longhorn population after its establishment
in 1927 (data from Halloran 1962).

Year	Bulls	Cows	Source
1928	--	3	--
1931	2	--	Mexico
1936	2	--	Mexico
1941	10	--	Mexico
1946	--	12	Mexico
1949	1	--	Texas
1951	8	--	Texas
1965	1	--	Texas
Total	24	15	

refuge policy to not breed longhorn cows until they are at least
2 years old.

Males are classified as "bulls" when yearlings but nothing was
found in the refuge reports which would indicate the age at which they
attain sexual maturity or perform first service. Most of the males
in the herd are castrated within a few months after birth and are only
retained for public viewing.

Calving Performance of Longhorn. Data on the productivity of
individual longhorn cows is readily attainable during the fall roundup
because close scrutiny of individual cows is undertaken not only to
determine their reproductive status but also to ascertain whether or
not they give birth to calves possessing desired physical traits.
Cows which are nonproductive or which give birth to undesirable
calves are generally culled from the herd.

Single births are the rule for Wichita longhorn. No reference
to multiple births appears in the available records. Since it has been
refuge policy (prior to 1957) to combine females of all age classes
when reporting reproductive information, we were unable to ascer-
tain whether or not females breeding as yearlings were more or less
likely to bear a calf than older females.

Sex composition of the calf crop has not been reported in all
years but the information available (Table 3) indicates equal numbers
of male and female calves is the general rule. The percentage of

Table 3. Sexual composition of calf crops for longhorn cattle on the
Wichita Mountains Wildlife Refuge.

Year	Male Calves	Female Calves	Total
1927	1	3	4
1928	6	7	13
1929	7	9	16
1930	9	12	21
1931	12	15	27
1932	10	12	22
1933	18	11	29
1934	20	16	36
1943	25	18	43
1951	38	30	68
1952	39	42	81
1954	43	34	77
1955	52	52	104
1964	43	54	97
1965	49	53	102
1972	52	49	101
Total	424	417	841
Percent	50	50	

males and females in the calf crop may vary between years, however.

Reproductive success (percentage of cows producing a calf) in the longhorn herd has fluctuated over time (Fig. 4). In many ways, the calving success for longhorn on the refuge was similar to that described above for bison. For the first few years after longhorn were established on the Wichita, reproductive success in the herd declined, finally stabilizing for a brief period during the late 1930's and early 1940's. Like the reproductive pattern of bison, reproductive rates for longhorn cattle increased substantially during the 1940's. Unlike the reproductive rates observed for bison, however, reproduction by longhorn cattle has been relatively constant since the early 1950's. This is thought to be due in large part to the constant herd size maintained over the same time span.

The lowest calf crop recorded for longhorn cattle on the Wichita (41 calves per 100 cows) occurred in 1936 while the herd was still being held in the Buffalo Pasture. It seems likely that the same husbandry actions believed responsible for the increase in bison reproductive rates during the 1940's contributed to the increase in longhorn calving rates as well. Vaccination of longhorn calves for brucellosis began in 1944 (Bartnicki 1972) and, like bison, the stocking pattern for longhorn cattle changed after 1938 when the Buffalo Pasture was modified.
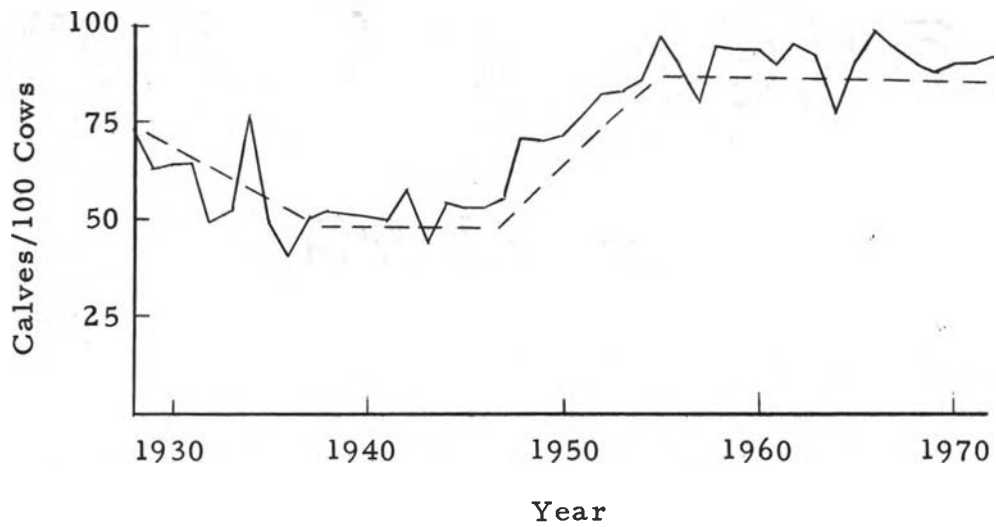
Figure 4. Historical trend in calving rates for longhorn cattle on the Wichita Mountains Wildlife Refuge. Percentages reflect the number of cows which produced calves.

Synthesis of Longhorn Reproductive Functions. Reported information on calf production by longhorn cattle was converted to density-dependent (linear regression) functions to express the relation between calving rate and herd size. Least-squares regressions calculated for calving data recorded between 1927 (date of introduction) and 1938 suggested two distinct reproductive trends. During the early part of the period (1927 to 1934), the linear regression $Y = .629 - .0008(X)$ best described reported longhorn natality as determined by correlation tests (Fig. 5-A). The "X" in the expression refers to herd size at breeding. During the latter portion of the period (1935 to 1938), the regression for longhorn productivity became steeper (Fig. 5-B), indicating longhorn calving rates declined more rapidly with increased herd size than they did earlier in the period.

The year 1938 brought about a change in the range ecology of Wichita longhorn and reproductive functions synthesized from field data reported after that date reflect that change. Prior to 1938, the herd was held in the Buffalo Pasture but was later released into an area roughly four times larger in total grazing space. Changes in grazing conditions may explain, at least in part, why regression equations for calving data gathered between 1939 and 1954 reversed the trend noted in the 1930's. Instead of calving rates declining with increased herd size, as they did during the 1930's, calving rates
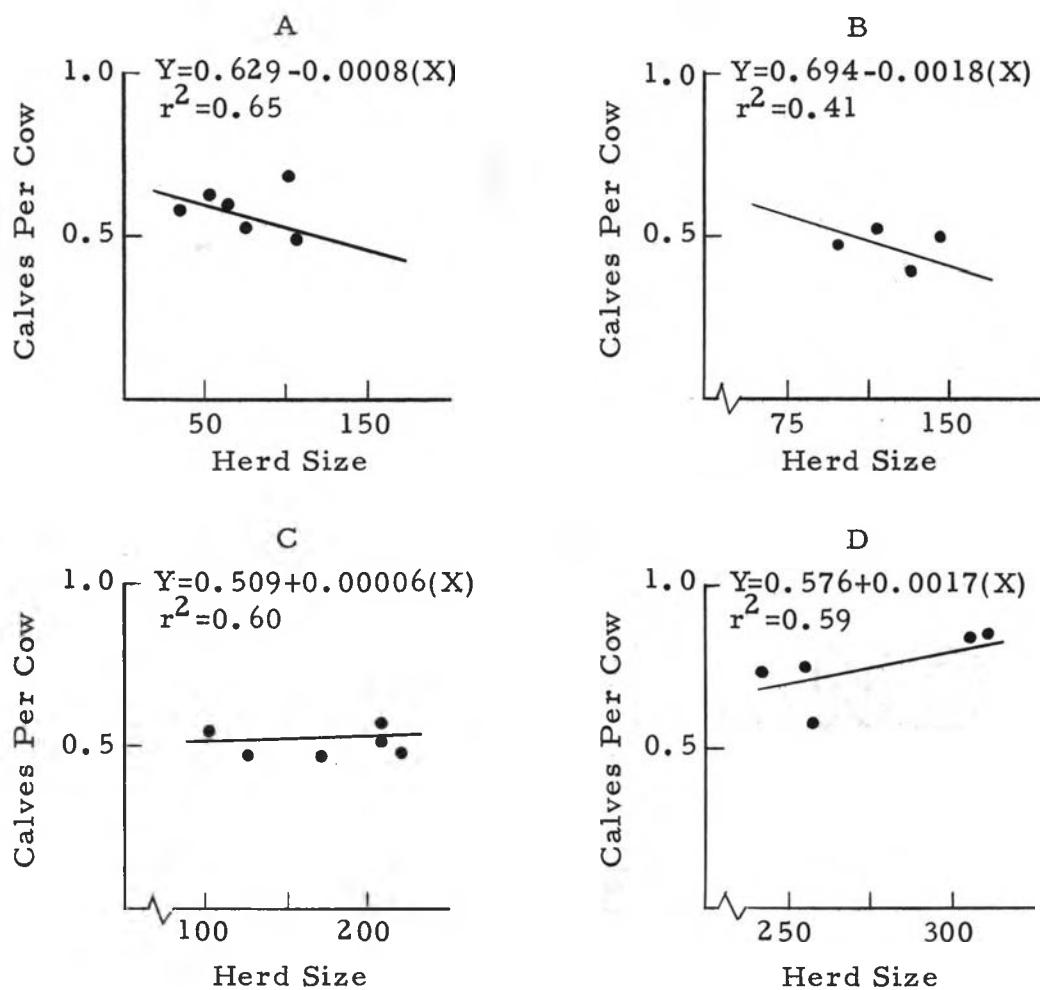
Figure 5. Least-squares regression formulae which best described longhorn cattle reproduction over time on the Wichita Mountains Wildlife Refuge. Time periods: A. 1927-1934, B. 1935-1938, C. 1939-1944, D. 1945-1953.

measured during the 1940's and 1950's increased as herd size increased. The expression $Y = .509 + .00006(X)$ best described calving rates reported between 1939 and 1944 (Fig. 5-C) but calving rates increased at a faster rate between 1945 and 1953, as evidenced by the greater positive slope of the regression for that period (Fig. 5-D). An average reproductive rate of .906 calves per cow was synthesized for longhorn cattle between 1954 and 1972.

Natural Losses

Longhorn deaths resulting from natural causes have been reported in most years (Table 4). Percent natural loss has varied greatly between years, being highest during the first few years immediately following the longhorn's introduction to the Wichita refuge. Herd size was small during this period and the occurrence of one or two natural deaths yielded high mortality percents. Percent mortality decreased as herd size increased such that the average loss between 1927 and 1972 was about 2.5 percent. This average may be biased to some degree, however, because of lack of information on mortality losses during 1934 to 1943. It is not known whether natural mortality during that interval was minimal or whether it simply was not observed and reported.

The mortality agent responsible for the death of individual longhorn has been reported less frequently than total loss. Often the immediate cause of death was not determined (or reported) and, in

Table 4. Summary of natural mortality data available for longhorn cattle, Wichita Mountains Wildlife Refuge.

Year	Bulls	Cows	Calves	Unspecified	Total	Percent
1927	1	1			2	6.3
1928	0	2			2	4.6
1929	0	4	1		5	9.4
1930	1	1			2	2.8
1931	1	1	3		5	6.6
1932	0	1	1		2	2.1
1933	0	2	1		3	3.0
1944	3				3	1.3
1945			1		1	.4
1946	2			6	8	3.2
1947	2		1	6	9	3.6
1948	2	1	2	3	8	3.6
1949	3		5	3	11	3.9
1950	1	2	1	6	10	3.4
1951	2		1		3	1.2
1952	2				2	.5
1953	5	1	2		8	2.5
1954		1			1	.3
1955		1	1		2	.7
1956	1		1	1	3	.7
1957	2		2	3	7	1.8
1960				1	1	.3
1961				4	4	1.3
1962				5	5	1.7
1963			4	4	8	2.7
1964				8	8	2.7
1965				5	5	1.7
1966				4	4	1.3
1967				3	3	1.0
1968				6	6	2.0
1969			2		2	.5
1970				1	1	.3
1971			7	4	11	2.6
Totals	28	18	36	73	155	
Mean						2.48

some cases, the animal simply disappeared, its fate remaining un-
known. But the few instances in which a specified mortality agent
was given provided the following frequencies: poachers (15), acci-
dents (8), old age (7), disease (6). No losses to bobcats (<u>Lynx</u> <u>rufus</u>)
or coyotes (<u>Canis</u> <u>latrans</u>), the two principle wild mammalian
predators on the refuge, have been reported.

Longhorn Harvest Information

Harvest information used to simulate the history of the Wichita
longhorn population was based upon harvest totals reported by
Halloran (1964) plus information compiled from annual narrative
reports. Since there was little reported information on the age
structure of annual harvests, age structure of the harvest was
assumed to be proportional to the size of each age class (no selec-
tivity between age classes).

Elk Field Data

The elk or wapiti is indigenous to the Wichita Mountains region.
Halloran (1963) cited various early records which told of elk being
hunted on the Wichita as late as the 1880's. Over-harvesting is
believed to have been the reason for the species disappearance from
the area.

Elk were reintroduced to the Wichita Mountains in 1911 with
the release of 1 bull and 4 cows brought to the refuge from Jackson

Hole, Wyoming. Fifteen more elk, 3 bulls and 12 cows, were added in 1912, also obtained from Jackson Hole. The present herd descended entirely from these 20 animals.

The subspecies of elk currently found on the Wichita is believed to be different from the native subspecies. According to Halloran (1963), Rocky Mountain elk (C. canadensis nelsoni) were transplanted to the refuge and replaced the native Merriam's elk (C. canadensis merriami).

For the most part, elk occupy the more-inaccessible portions of the refuge. A few animals are maintained in exhibitation pastures near the main tour routes but most elk have moved into pastures away from these areas. As a consequence, the major recreational benefit derived from the herd is sport hunting.

Census Effort

The techniques used to census the Wichita elk herd during the early years are obscure in the refuge's files although ground counts were probably used. Helicopter counts have been in use since about 1955. Aerial estimates are made in winter (January through March) and are flown during early morning, concentrating on areas which receive heavy use from elk. The objective of the counts is to observe as many elk as possible in order to estimate the total refuge population. The accuracy of these aerial counts is untested but appears to vary with observer and weather conditions. Counts in

recent years are thought to be accurate by the refuge biologist but earlier counts were undoubtedly low. Throughout much of the 1960's, a correction factor of 15 percent of the number of elk observed was added to the final tally to compensate for elk present but not seen.

Ground counts undertaken to sex and age the refuge herd have been in use since 1969. These counts, in comparison to the aerial counts, are made during late summer or early fall during the rut. The refuge biologist records all elk sightings and classifies individuals seen as bulls, cows or calves. Breeding harems are located and classified to obtain information on calving rates. The results of both aerial and ground counts are used to cross-check and update an inventory sheet maintained on the elk herd which documents all additions to and removals from the herd.

Harvest

Following the reintroduction of 20 elk to the refuge in 1911 and 1912, habitat conditions proved suitable and the herd increased to 300 head by 1925. Herd control was deemed necessary at that point and a program of annual herd cropping was initiated. For nearly 50 years, surplus animals were sold alive for restocking, donated or butchered for meat. Sport hunting was adopted in 1969 as the means of regulating size of the herd.

Accurate records have been maintained on elk removed from the refuge. Sex structure of the harvest has been recorded in most

years but, until recently, little information was available on the age of the animals harvested other than Halloran's (1957) general statement that refuge policy prohibited the disposal of elk less than $2\frac{1}{2}$ years of age. Elk disposals between 1925 and 1972 for which sex information was recorded totaled 2775. Of that total, 1294 (47 percent) were bulls and 1481 (53 percent) were cows.

Reproductive Biology

Breeding Age. The examination of reproductive tracts removed from butchered elk and also from cows taken by hunters provides information on the breeding chronology of Wichita elk. Data collected since 1961 (Fig. 6) reveal the percentage of cows from each age class found to be visibly pregnant at the time of harvest (November and December).

Based upon the evidence available, it appears as though Wichita elk seldom conceive when they are $1\frac{1}{2}$ years old. Of the 71 yearling cows harvested between 1969 and 1973, only 5 (7 percent) were reported pregnant. A substantially larger percentage of the $2\frac{1}{2}$-year-old cows conceive but prime breeding age for cows in the Wichita Mountains seems to occur at 3 years of age.

These findings on the Wichita are not entirely consistent with data reported from other areas. For example, there appears to be a lower incidence of pregnancy among younger cows ($1\frac{1}{2}$ and $2\frac{1}{2}$ years old) on the Wichita than there is among cows of the same age in herds
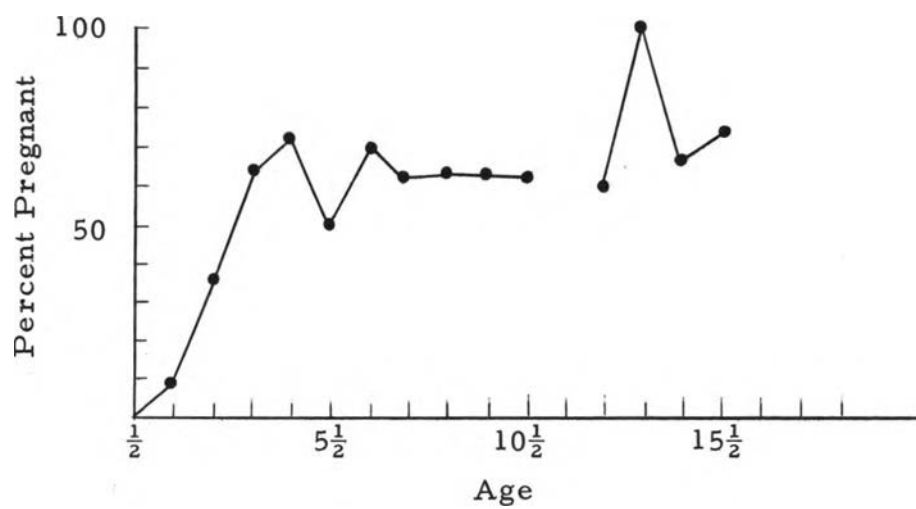
Figure 6. Incidence of pregnancy among cow elk of various ages on the Wichita Mountains Wildlife Refuge. Data are from cows harvested 1961-1967 and 1969-1973.

of the Sun River drainage in Montana and Yellowstone National Park
(Table 5). Pregnancy rates among older cows seem to be somewhat
uniform between the three areas however.

Annual Variation in Incidence of Pregnancy. The amount of
year-to-year variation in pregnancy rate for elk on the Wichita refuge
is substantial (Table 6). The pattern is similar to that pointed out
above for the annual variability of bison calving rates. Judging from
the respective standard deviations, the variability in pregnancy in-
cidence for 2-year-old cows is greater than that for older cows.

More 2-year-old cow elk have been reported pregnant since
1969 than during the period from 1961 through 1968. Granted the
sample sizes are too small to draw any definite conclusions. But, if
these findings do indicate a higher incidence of pregnancy among
2-year-old cows after 1969, that increase would correspond roughly
with a substantial reduction in the refuge herd. During December
1965, there were approximately 1100 elk on the refuge. This
estimate was derived through computer simulation and is justified in
a later section of the report. Subsequent efforts by the refuge staff
reduced the herd size by about 60 percent, such that in December
1970, (postseason) only 460 elk remained on the refuge (Bartnicki
1973). The interesting question is whether or not this herd reduction
in any way contributed to the higher incidence of pregnancy among
younger cows. Evidence gathered in other studies indicates there
could be a cause-and-effect relationship between the two events.

Table 5. Comparison of pregnancy rates for elk from different areas. Values are percent of the age class pregnant.

Area	Age			Source
	$1\frac{1}{2}$	$2\frac{1}{2}$	$3\frac{1}{2}+$	
Sun River	26	64	79	Knight 1970
Yellowstone Park	7	93	91	Cheatum and Gaab 1952
Wichita Mountains	7	35	67	---

Table 6. Comparison of pregnancy rates for elk on the Wichita Mountains Wildlife Refuge between years.

Year	2-Year-Old Cows			Mature Cows		
	No. Examined	No. Pregnant	%	No. Examined	No. Pregnant	%
1961	7	0	0.0	58	23	39.6
1962	--	--	--	27	13	48.1
1963	--	--	--	18	9	50.0
1964	2	0	0.0	38	29	76.3
1965	6	1	16.6	46	27	58.7
1966	11	0	0.0	118	94	79.7
1967	12	0	0.0	126	67	53.2
1968	--	--	--	--	--	--
1969	2	2	100.0	28	16	57.1
1970	2	0	0.0	35	12	34.3
1971	1	0	0.0	30	47	94.0
1972	5	3	60.0	77	42	54.5
Mean			19.6			58.7
S.D.			36.1			17.0

Buechner and Swanson (1955) found a high incidence of pregnancy among yearling elk in southeastern Washington following a reduction in herd level. In a similar manner, Greer (1966) discovered fertility rates for yearling elk in Yellowstone National Park increased from 9 percent to 28 percent following a herd reduction which lowered winter herd size from 10000 to 5000 elk. Although pregnancy rates of yearlings increased, Greer's study found that the pregnancy rate of mature (2-15 years old) elk were consistent between years, ranging from 95 to 100 percent. Thus, the small amount of information from the Wichita is inconsistent with Greer's findings in that pregnancy rates of 2-year-old cows seems to have increased following herd reduction. It is unknown to what extent the Wichita reduction may have affected the incidence of pregnancy among yearling elk on the refuge but a few (5 of 71) yearlings have been found pregnant since the herd reduction occurred.

Calving Rates. Information about elk calving rates is poor in the files prior to 1969 since few efforts were made to gather such information. Throughout much of the 1960's, the policy was to assume a constant rate of increase in the herd. An annual increase of 17 percent of the known herd size was assumed between 1960 and 1965 but the estimate was raised to 25 percent between 1966 and 1968.

Although calving records are fragmentary and inconsistent, there are some accounts of the number of calves seen in the herd. In

other instances, estimates of the total number of calves produced by the herd were made. Lacking, however, and needed to determine a calving rate, is the number of cows which produced those calf crops.

In order to estimate a herd calving rate for elk, the approach used in this study was to first estimate the number of cows in the herd in the following manner. It was assumed that approximately 50 percent of the herd would be females. This assumption seemed reasonable because, as pointed out above, bulls made up about 47 percent of the harvest. Removing fewer bulls than cows from a herd with a 50:50 sex ratio would, over time, cause a gradual increase in the male segment. But also taken into consideration in these calcu- lations was evidence that bull elk on the Wichita sustain a slightly higher rate of natural mortality than do the cows. More discussion of this point is presented below. Therefore, the combined effects of hunting and natural attrition would be expected to maintain the 50:50 sex ratio.

Next the number of breeding-age cows was calculated by assuming that 20 percent of all females do not reproduce. Included in this group would be all yearling cows plus any additional cows too old to bear a calf. This percentage has been used by the refuge biologist in his calculations (Bartnicki 1972a) and therefore was adopted for use here.

The resulting calving rates (calves per 100 cows) obtained from the procedure are plotted in Fig. 7. Caution should be exercised in their interpretation. The estimates are believed accurate enough to indicate the general trend in elk calving rates over time, but the accuracy of a value for any given year should be accepted with discretion.

Based upon this analysis, the historical trend in calving rates for Wichita elk is similar to the patterns previously described for bison and longhorn. As noted for those species, there appears to be an increase in elk calving rates during the 1940's. This is followed by a period during the 1950's and 1960's in which calving rates declined.

The average preseason calving rate reported between 1969 and 1972 was about 40 calves per 100 cows. This seems low in comparison with calf:cow counts found in some areas but is higher than those found in others (Table 7).

Elk Calving Rate Functions. If we assume that the elk calving rates calculated above are reasonably correct, then it appears that two distinct calving-rate patterns occurred on the Wichita between 1913 and 1972. During the period 1913 through 1940, the function which best described the calving data (Fig. 8-A) was $Y = 1.0 - .002(X)$. The "X" in the equation represents breeding herd size. A similar function, $Y = 1.03 - .0009(X)$ shown in Fig. 8-C, was
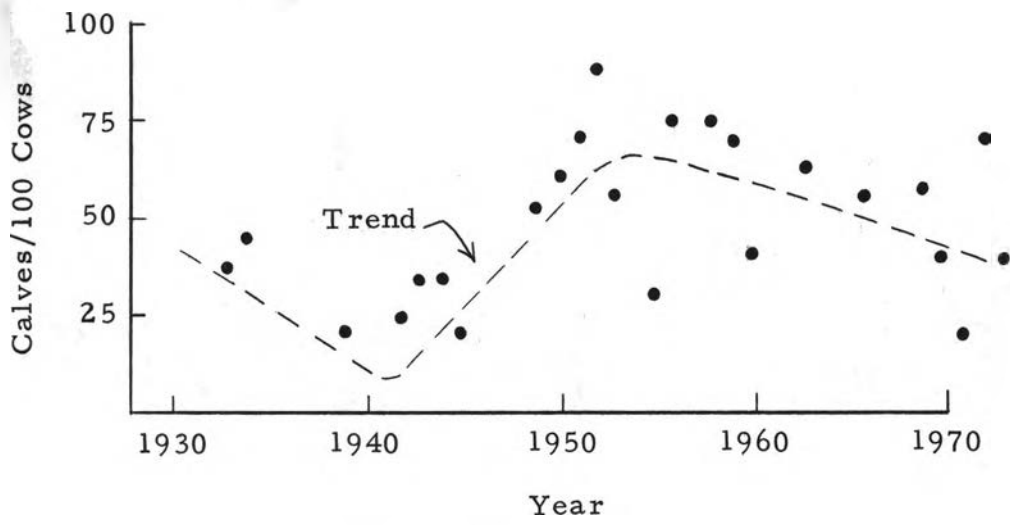
Figure 7. Historical trend in calving rates for elk on the Wichita
Mountains Wildlife Refuge.

Table 7. Comparison of elk preseason calf:cow ratios observed on
the Wichita Mountains Wildlife Refuge with those reported
from other areas. (Data for the Wichita refuge are from
Bartnicki 1973.)

Location	Calves Per 100 Cows
A. Wichita Mountains	
Year	
1969	28
1970	39
1971	19
1972	72
Average	39.5
B. Other Herds	
White River (Boyd 1970)	63
Cache National Forest (Kimball and Wolfe 1974)	57
Hardware Ranch Management Unit (Follis and Spillett 1974)	53
Sun River (Knight 1970)	30
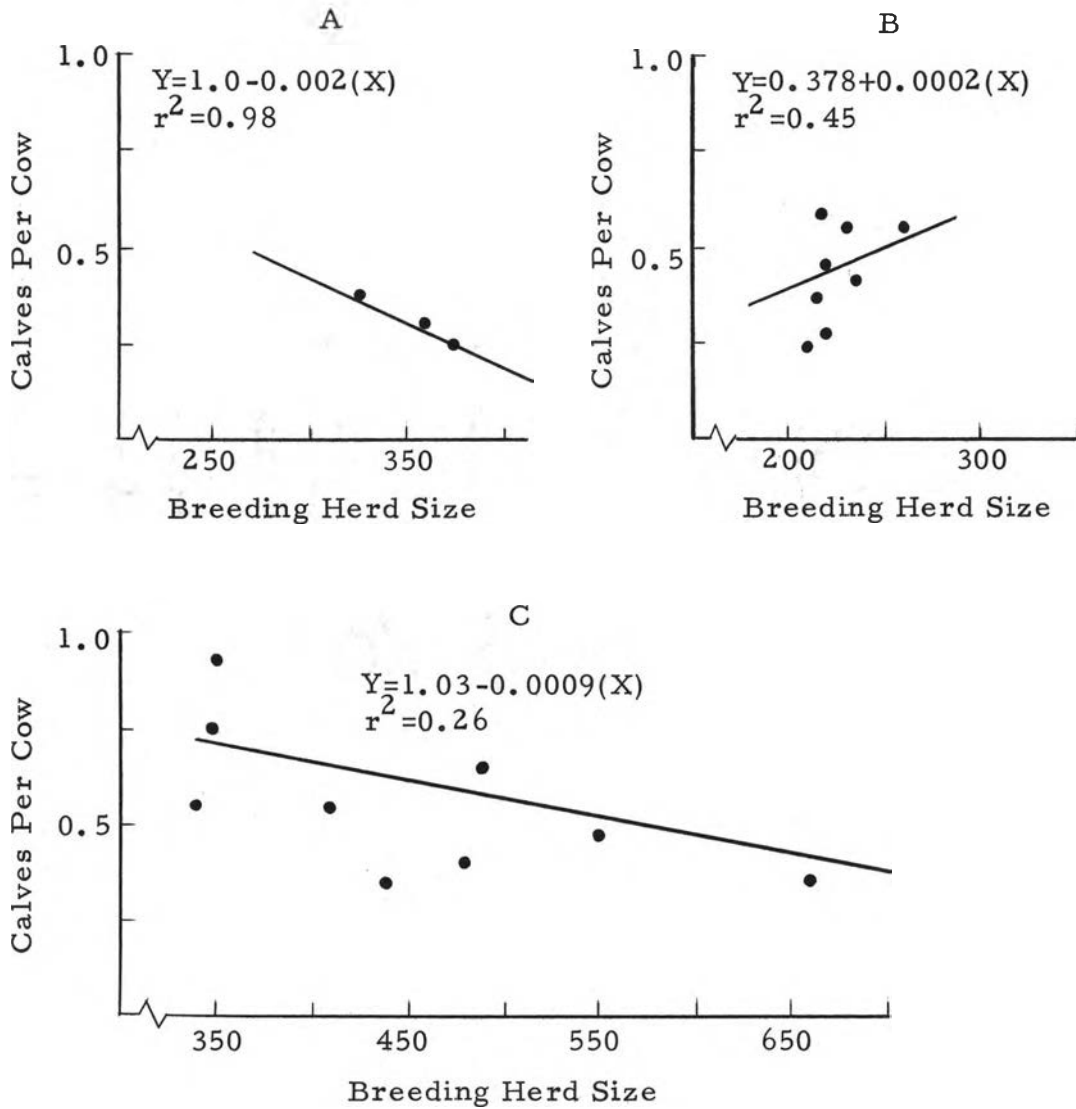
Figure 8. Least-squares regression formulae describing the functional relations between elk calving rate and breeding herd size on the Wichita Mountains Wildlife Refuge. Time periods: A. 1913-1940, B. 1941-1954, C. 1955-1972.

calculated for calving rates compiled during the period 1955 through
1972. Both of those calving functions have negative slopes, indicating
that elk calving rates declined as breeding herd size increased.

The second distinctive pattern in elk calving-rate trend occur-
red during the intermittent years 1941 through 1954. The linear
function calculated for calving rates during those years (Fig. 8-B)
was $Y = .378 + .0002(X)$ whose positive slope indicated that, unlike
the pattern for the early and late periods, elk calving rates increased
as herd size grew.

Reproductive Failure. As mentioned above, two independent
estimates of elk reproduction are made in each breeding cycle. The
first, a determination of pregnancy rate, is based upon examination
of materials collected from elk shot during the hunt. The second
measure of reproductive effort is estimates of calf:cow ratios made
during fall. A comparison of these two indicators would provide an
assessment of reproductive failure; i.e., it would provide an indica-
tion of fetal losses and/or calf losses between the time of the hunt
(December) and the time calf:cow counts are made in August and
September.

In order to carry out the analysis, two assumptions had to be
made. First, it was necessary to assume that age structure of the
female harvest was representative of the entire female herd.
Secondly, it was assumed that no mortality occurred between the time

the two estimates were made. Mortality did occur and sampling error (i.e. hunter selectivity) may have occurred. Nonetheless, if these factors remain relatively constant from year to year, the assumptions should hold and the analysis should be valid at least on a relative basis.

The analysis (Table 8) detected little evidence of reproductive failure. Only during 1 of the 3 years examined was the calf:cow ratio observed in the field noticeably different from what was expected. The small sample size (i.e. female harvest) in 1969 may be responsible for the discrepancy between observed and expected calving rate rather than any biological events.

Follis and Spillett (1974) reported a similar investigation of winter pregnancy rates and subsequent calf:cow ratios for an elk herd wintering near Logan, Utah. Results of their study are similar to those presented here. My results support their belief that pregnancy information provides a valuable forecasting tool for herd productivity so long as the assumptions cited above remain valid.

Natural Mortality

Estimates of natural attrition among Wichita elk are crude. Halloran (1963) reported an average of 12 animals lost to natural, accidental and poacher-related causes between 1925 and 1956. Reported herd size during the interval varied between 250 and 300 elk. Thus, if Halloran's estimate is correct, it implies a herd

Table 8. Comparison between observed and expected calf:cow ratios
for the Wichita Mountains Wildlife Refuge elk herd based
upon December pregnancy rates.

Year		Pregnancy Rate		Calves Expected
1969				
	31 Matures	0.75	31 Matures	23
	7 Yearlings	0.00	7 2½ Yr. Olds	0
	1 Calf	0.00	1 Yearling	0
			39 Cows	23 Calves

Twenty-three (23) calves per 39 cows equals an expected
calf:cow ratio of 59:100. Observed ratio was 39:100.

1970				
	N.D.[1]	N.D.	N.D.	N.D.

1971				
	51 Matures	0.92	51 Matures	47
	12 Yearlings	0.08	12 2½ Yr. Olds	1
	4 Calves	0.00	4 Yearlings	0
			67 Cows	48 Calves

Forty-eight (48) calves per 67 cows equals an expected
calf:cow ratio of 72:100. Observed ratio was 72:100.

1972				
	82 Matures	0.55	82 Matures	45
	11 Yearlings	0.00	11 2½ Yr. Olds	0
	20 Calves	0.00	20 Yearlings	0
			113 Cows	45 Calves

Forty-five (45) calves per 113 cows equals an expected
calf:cow ratio of 40:100. Observed ratio was 38:100.

[1]Sample size too small to make calculations.

mortality rate of 4 to 5 percent annually, a rate only slightly higher than what has been noted previously for longhorn cattle and comparable to that of bison on the refuge.

There were no data available with which to compare the mortality level of bulls with that of cows. However, it is suspected that bull mortality rate was higher than that of cows. The first indication of possible disproportionate mortality on the sexes became apparent while simulating herd history. Under the assumption of equal mortality on the sexes, the model failed to generate herd sex ratios observed in the field. Then, during a subsequent meeting with the refuge staff, the refuge biologist mentioned that seldom are bulls over 10 years old taken during the hunt. An examination of the age distribution of elk shot on the refuge between 1969 and 1973 (Fig. 9) revealed that of the 299 bulls shot, 9 (3 percent) were at least 10 years of age. Conversely, 22 of the 338 cows (6 percent) were 10 years or older. Data for the 1971 hunt, a year in which only antlerless elk were legal, were omitted from the analysis.

These Wichita observations are similar to those reported by Flook (1970) for wapiti in Canada. He observed that the maximum age of any bulls to which precise age was assigned was 14 years whereas cows up to 19 years were found in the herd. From his observations, he concluded that the mortality rate of male wapiti became higher than that of females sometime after $1\frac{1}{2}$ years of age.
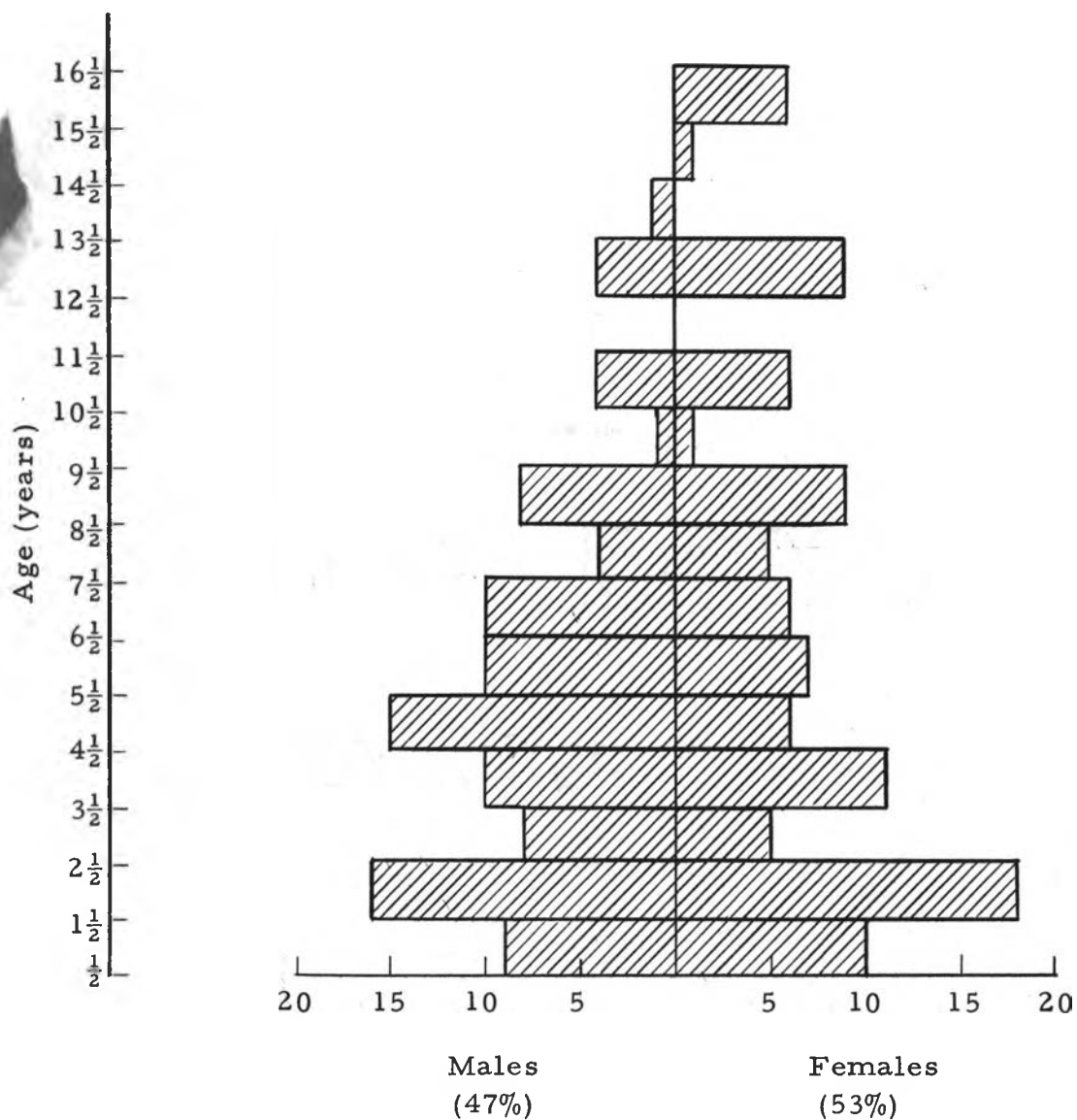
Figure 9. Age distribution of elk shot on the Wichita Mountains Wildlife Refuge between 1969 and 1973. Data for 1971 have been omitted.

His data also suggested that, after about 7 years of age, the mortality of bulls increased markedly relative to that of cows of equal age. One tentative explanation given for the higher male mortality was that physical stress of the rut weakened the bulls immediately prior to winter when environmental conditions were most severe.

White-tailed Deer Field Data

White-tailed deer are also indigenous to the Wichita Mountains. The current refuge herd has descended entirely from the animals on the area when the refuge was established in the early 1900's.

Three separate herds are identified in the immediate vicinity of the refuge and are often referred to collectively as the Comanche County deer population. Separate herds are distinguished for the deer found on the Wichita refuge, those found on Fort Sill Military Reservation and those found on non-federal lands adjoining the refuge and Fort Sill.

Deer are maintained on the refuge primarily for public viewing. Sport hunting for deer has never been allowed, although numerous deer were removed from the refuge by live-trapping during 1945 through 1964. Although not practiced on the refuge, deer hunting has been common practice on lands contiguous with the refuge as well as on Fort Sill. Thus, if deer movements between these areas are substantial, the refuge herd could be considered a hunted population.

However, movements by deer between Fort Sill and the refuge are believed to be minimal (George Johnson, personal communication). This is probably true of the other areas as well.

The following analysis of the Wichita herd will be restricted to the period 1955 through 1973 owing to the lack of demographic information prior to this period. Likewise, insufficient information was available to determine to what extent results obtained for the refuge herd apply to other herds in the same vicinity.

Census Techniques and Sampling Effort

Two separate techniques have been used to estimate deer numbers on the refuge. Steele (1969), for his study of deer ecology in Comanche County during 1966 and 1967, used the Hahn deer cruise-census method. He neglected to describe the version of the technique used but it was most likely similar to the technique described by Teer et al (1965).

Steele made two counts during each sampling period, one during the fall (September through December) and another during spring (March through June). He obtained an idea of the precision of his estimates by subtracting suspected winter losses from the fall count and comparing the result with the spring count.

A second method of counting deer on the refuge has been used by the refuge staff and is similar to the Hahn cruise-census method in that transects were also used. Deer sightings were made while

driving a motor vehicle over an established route. The number of deer actually seen was multiplied by a conversion factor to account for deer present but not seen.

The accuracy of these census methods is unkonwn, but estimates made during the 1950's and 1960's with the conversion-factor method have been questioned (E. A. Bartnicki, personal communication) because of the large conversion factors used (in some cases over 400).

Population Density and Changes in Herd Level

The number of deer on the refuge at the time of its establishment is unknown but 200 were reported in 1914 (Anonymous 1914). Herd growth was apparently slow during the early days of the refuge because a census made in 1926 found 250 deer on the refuge, an increase of only 25 percent over the 1914 level. The slow rate of herd growth was attributed to heavy losses resulting from poaching, predation and disease (Anonymous 1927a).

Population growth must have increased during the 1930's and early 1940's because by December 1945, the refuge population had grown to an estimated 800 deer. A second period of rapid herd growth occurred between 1955 and 1961 when the herd increased from 1250 (December 1955) to an all-time high of 2100 (December 1961).

Judging from the available information, deer would be expected to make the most use of areas of the refuge similar to the Rocky

Mountain Escarpment sites described by Allred (1955). The refuge biologist, however, believes the entire refuge should be considered as deer habitat (E. A. Bartnicki, personal communication). If we assume that deer are distributed evenly throughout the area, the maximum concentration of deer (winter density) would have been about 1 deer per 11 ha or 3.5 deer per 100 acres. These estimates suggest fewer deer per unit area on the Wichita than in the Llano Basin of western Texas, an area about 300 miles southwest of the refuge. Teer et al (1965) reported white-tailed deer densities averaged 14.4 deer per 100 acres in that area between 1954 and 1961.

Live Trapping

A rapid buildup of the Wichita herd occurred in the late 1950's, prompting efforts to constrain herd size through increased live trapping (Halloran 1964). Thus, during the trapping seasons of 1955 through 1964, 3564 deer were trapped by the Oklahoma Department of Wildlife Conservation and released in other areas of the state. The removals included 1261 bucks (35 percent), 1447 does (41 percent) and 856 fawns (24 percent).

The effect of the live trapping was constrained herd growth. However, when trapping operations ceased in 1964, the herd began an unexpected decline that continued through the 1960's. According to E. A. Bartnicki (personal communication), the herd declined to about 500 deer and has fluctuated around that density since about 1971.

Theoretically at least, the deer population should not have declined after live-trapping operations were terminated. The herd should have either maintained itself or started growing. The decline was not confined to the Wichita refuge because declines occurred as well on Fort Sill and the adjoining areas of Comanche County (Steele 1969). In order to account for such wide-spread similarities, one would have to conclude that some ecological change occurred in the region during the 1960's which left conditions detrimental to white-tailed deer, thereby initiating the declines in herd level. Tentative explanations are discussed below.

Reproduction

Ovulation and Conception. Steele (1968) examined fetal deer taken from does on the refuge in an effort to determine the time of year during which most of the breeding activity takes place. Although he examined only a few fetuses (Table 9), he concluded that the peak of breeding activity for white-tailed deer in Comanche County occurred between 1-14 November.

Severinghaus and Cheatum (1965:62) gave the gestation length for white-tailed deer as 189 to 222 days. Based upon Steele's estimates of peak conception, it therefore appears as though peak fawning activity on the refuge should occur in mid-June.

Other data reported by Steele (1969a) provided information on the ovulation and pregnancy rates for white-tailed deer in Comanche

Table 9. Approximate age and data of conception for white-tailed deer during 1967, Wichita Mountains Wildlife Refuge (after Steele 1969).

Collection Date	Approximate Age in Days	Projected Conception Date
January 14	56	November 22
January 17	65	November 11
January 23	78	November 7
January 28	80	November 9
February 4	65	November 30
February 18	90	November 10
February 22	105	November 9

County. Steele examined 17 ovaries and found a total of 11 corpora lutea of pregnancy (Table 10) as well as 11 fetuses. Because of the small sample size, (seven deer) Steele's findings are probably little more than suggestive of the true fetal mortality rate but they indicate 100 percent fetal survival to the time Steele made his collections in January and February. Fetal losses may occur after this time.

Fawning Rates. In addition to the density estimates for the Wichita discussed above, there have also been attempts to ascertain fawning rates for deer on the Wichita. These estimates have been made in a manner similar to the density estimates. All deer seen while driving over established routes in July and August were classified as bucks, does or fawns. From these observations, buck:doe and fawn:doe ratios were calculated. Because no attempts have been made to distinguish yearling does during the counts, it was impossible to determine from the information available to what extent yearling does on the refuge contributed to the fawn crop.

The average reported fawning rate for deer on the refuge between 1956 and 1972 was 52 fawns per 100 does (Table 11). Deer fawning rates were characterized by the same year-to-year fluctuations described previously for bison and elk. It is also apparent from information in Table 11 that deer fawning rates have declined steadily over the period. During the years 1956 through 1960, deer fawning rate averaged 63 fawns per 100 does compared to an average

Table 10. Relation between ovulation and pregnancy rates for white-
tailed deer in Comanche County, Oklahoma 1967-1968
(after Steele 1969a).

Doe Age	No. Ovaries Examined	No. Corpora Lutea of Pregnancy	No. Fetuses
$1\frac{1}{2}$	1	0	0
$2\frac{1}{2}$	4	2	2
$3\frac{1}{2}$	4	4	4
$4\frac{1}{2}$	4	2	2
$5\frac{1}{2}+$	4	3	3
Total	17	11	11

Table 11. Reported fawning rates for white-tailed deer on the
Wichita Mountains Wildlife Refuge derived from summer
classification counts. (From Steele 1969 and narrative
reports.)

Year	Number of Does	Number of Fawns	Fawns per 100 Does
1956	86	24	28
1957	86	48	56
1958	84	70	83
1959	--	--	--
1960	77	65	84
1961	60	25	42
1962	54	26	48
1963	34	15	44
1964	26	16	62
1965	24	13	54
1966	20	16	80
1967	19	9	47
1968	--	--	47
1969	--	--	44
1970	--	--	21
1971	--	--	25
1972	71	41	58
Mean			51.7

of only 37 fawns per 100 does over the 5-year period 1968 through 1972.

Fawn Survival. A consensus of opinion formulated from accounts contained in a variety of refuge reports seems to be that the decline in fawning rate may not have been as much a matter of poor fawn production as it was a matter of poor fawn survival. The trend during recent years seems to be high fawn production followed by high fawn mortality within the first few months after birth.

For example, Steele (1968) observed a ratio of 84 fawns per 100 does during July. A second estimate made in August indicated the ratio had dropped to 62 fawns per 100 does. More recently, Bartnicki (1970) noted that the fawn:doe ratio was close to 100 fawns per 100 does in his June estimates but observed that the ratio dropped to about 44 fawns per 100 does by September. Bartnicki's observations suggest a fawn mortality rate of about 60 percent between time of birth and early fall. Subsequent estimates derived through computer simulation substantiate Bartnicki's observations and are discussed in a later section.

Synthesis of Deer Reproductive Functions. Reproductive equations for deer were derived by first plotting winter fawn:doe counts against December population sizes and then calculating a least-squares regression. Reproductive functions computed in that manner exhibited negative slopes (reproduction decreased as herd size increased), indicative of density-dependent reproduction.

Two reproductive functions were calculated. The regression
$Y = 1.76 - .004(X)$ best described field data collected between 1955
and 1961 but reproductive rates decreased markedly during the 1960's.
The computed regression for fawn:doe information compiled 1963
through 1967 was $Y = .650 - .00022(X)$. As a crude comparison,
reproductive rates for white-tailed deer on the refuge during the
1960's declined to about one-third of what they were during the 1950's.
That reduction in reproductive rate is believed to be the consequence
of drought conditions on the refuge during the 1960's. Relative com-
parison of reproductive functions before and during drought are shown
in Figs. 10-A and 10-B, respectively.

Synthesis of Initial Population Size and Structure

Refuge files contain estimates for the total number of deer on
the Wichita during 1955, the first year simulated. But the files do
not contain sex and age data for the population at that time. To esti-
mate the sex and age structure of the initial simulated population, it
was necessary to derive sex and age information from field data
compiled during winter live trappings between 1955 and 1957. Since
each sex and age class was assumed to be trapped relative to its
abundance in the population (i.e. no selectivity for sex or age class),
the sex and age structure of the live trappings should be representa-
tive of the entire herd.

A

$Y=1.76-0.0004(X)$
$r^2=0.62$

B

$Y=0.650-0.00022(X)$
$r^2=0.96$
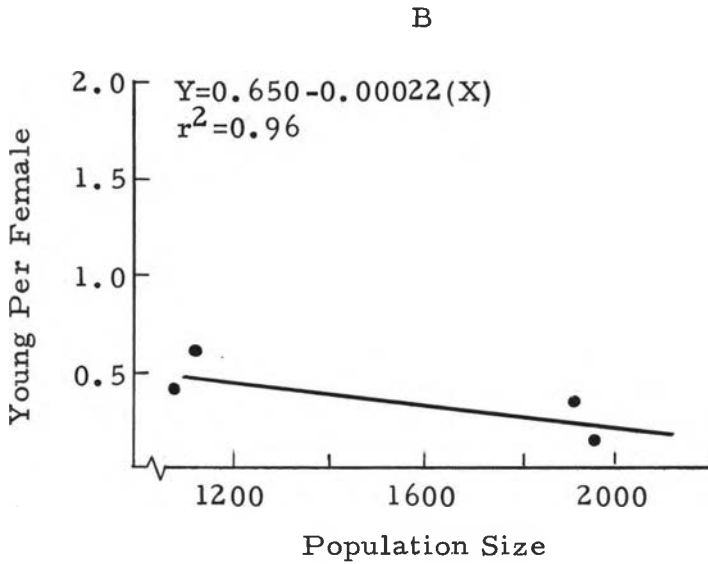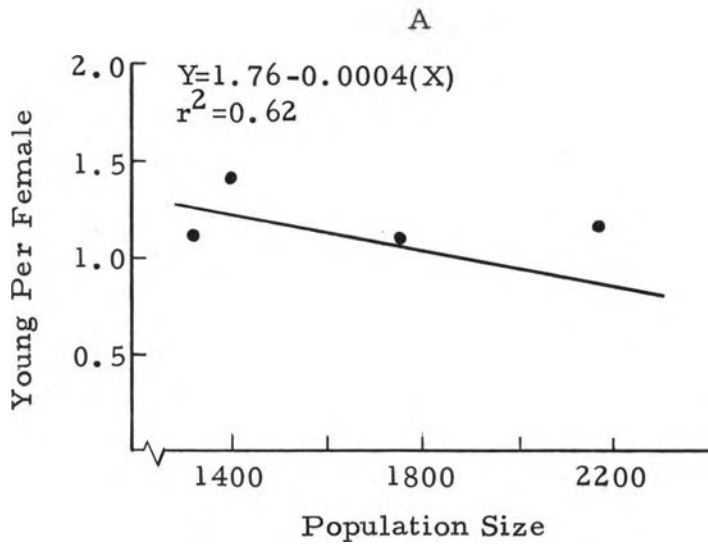
Figure 10. Linear regression formulae for reproductive rates for deer on the Wichita Mountains Wildlife Refuge. Time periods: A. 1955-1961 (before drought), B. 1963-1967 (during drought).

In this manner, the reported December 1954 herd of 1130 adult animals was broken down into bucks and does, distributed over 9 age classes. A fawn crop of 300 (about 26 percent of the adult herd total) was added to the adult population which gave a total initial population of 1430 deer. Sex and age structure of the initial simulated population is shown in Fig. 11.

Natural Mortality Information

Information on the magnitude of natural losses among deer on the Wichita is sparse. As a first approximation, mortality level for deer was set at 6 percent annually primarily because simulations for elk indicated the mortality in that population was about 6 percent annually. As was assumed for other ungulate herds on the refuge, the assumption was made that natural mortality affected both sexes equally.

Factors Influencing Deer Numbers

As noted previously, the decline in deer numbers during the 1960's was not limited to the Wichita refuge but occurred throughout the entire Comanche County area. Therefore, it seemed likely that, whatever factor(s) caused the decline, the area of influence was region-wide. The mechanism apparently involved decreased fawn production and/or fawn survival. The discussion which follows summarizes available information from refuge files on variables
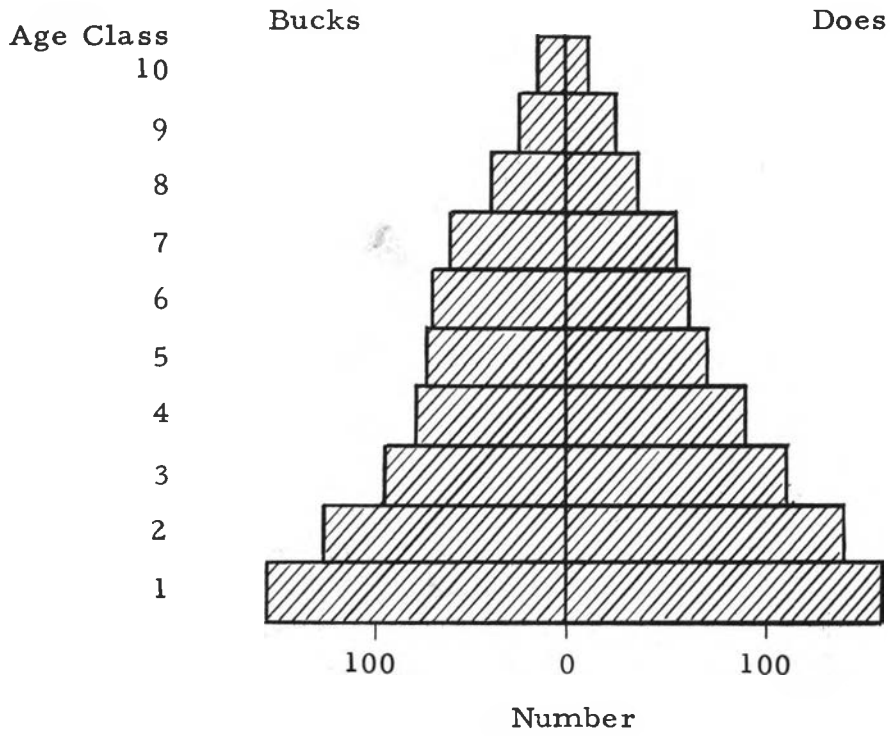
Figure 11. Initial population sex and age structure used in historic simulations for white-tailed deer on the Wichita Mountains Wildlife Refuge.

which might have contributed to the herd decline. No attempt is made
to identify the cause of the decline. The discussion merely reviews
what is currently known about factors shown historically to influence
herd biology.

Predation. Coyotes and bobcats are potentially important
predators of deer in Comanche County. Determination of the refuge's
population of those species is difficult, partly because of their ten-
dency to move onto and off of the refuge at various times. Steele
(1969) attempted to census predators on a 5000-acre (2025 ha) tract
in the Charons Gardens area of the refuge and found 6 to 8 bobcats
and 2 coyotes but speculated that more of both species were actually
present. Halloran (1956b) examined coyote-removal records from
the refuge and derived winter coyote population estimates ranging
from 100 to 218 for the entire refuge during the 1930's and 1940's.
More recently, the narrative report for 1971 included an estimate of
100 coyotes on the refuge during all or part of the year.

Food habits studies have shown rabbits (Sylvilagus sp) and a
variety of rodents to be the favorite prey species of coyotes in the
area. Stomach samples from 65 coyotes collected on the refuge
between 1937 and 1940 indicated rodents, invertebrates and rabbits
constituted 8.2, 16.5 and 18.5 percent of the coyote's diet respec-
tively. But Steele (1969) found significant percentages of deer tissue
in scats of both coyotes and bobcats examined in more recent years
(Table 12).

Table 12. Percentage of predator scats collected in Comanche
County, Oklahoma which contained deer tissues (from
Steele 1969).

	Year	Coyotes	Bobcat
	1965	25.4	26.8
	1966	30.3	12.7
	1967	16.6	11.8
Mean		23.8	17.1

Data suitable for assessing population impact of predation on the deer herd were not found in refuge reports. Certainly predators occur on the refuge and undoubtedly they kill deer. But the extent of those losses and whether or not they have influenced herd growth cannot be determined with the data available. Beasom (1974) conducted a study to determine the impact of coyote and bobcat predation on productivity of white-tailed deer in Texas. His observations showed a fawn:doe ratio of 0.47:1 on an area in which the predator population had been reduced compared to a fawn:doe ratio of only 0.12:1 on the control area. Similar results were obtained during the second year of investigation.

In light of Beasom's findings, it is interesting to note the history of predator-control efforts on the refuge. Coyote-control measures were in effect on the refuge at least from the 1920's until the mid-1950's (Fig. 12). Since that time, only sporadic efforts have been made to reduce coyote numbers. It is therefore conceivable that, once serious efforts at coyote control were stopped, the coyote population could have increased and been a contributing factor in the deer decline of the 1960's.

Drought. Mean annual precipitation has been shown to influence both the distribution and abundance of white-tailed deer. Teer et al (1965), in their study of deer in the Llano Basin of western Texas, found population distributed along an eastwest gradient. In that
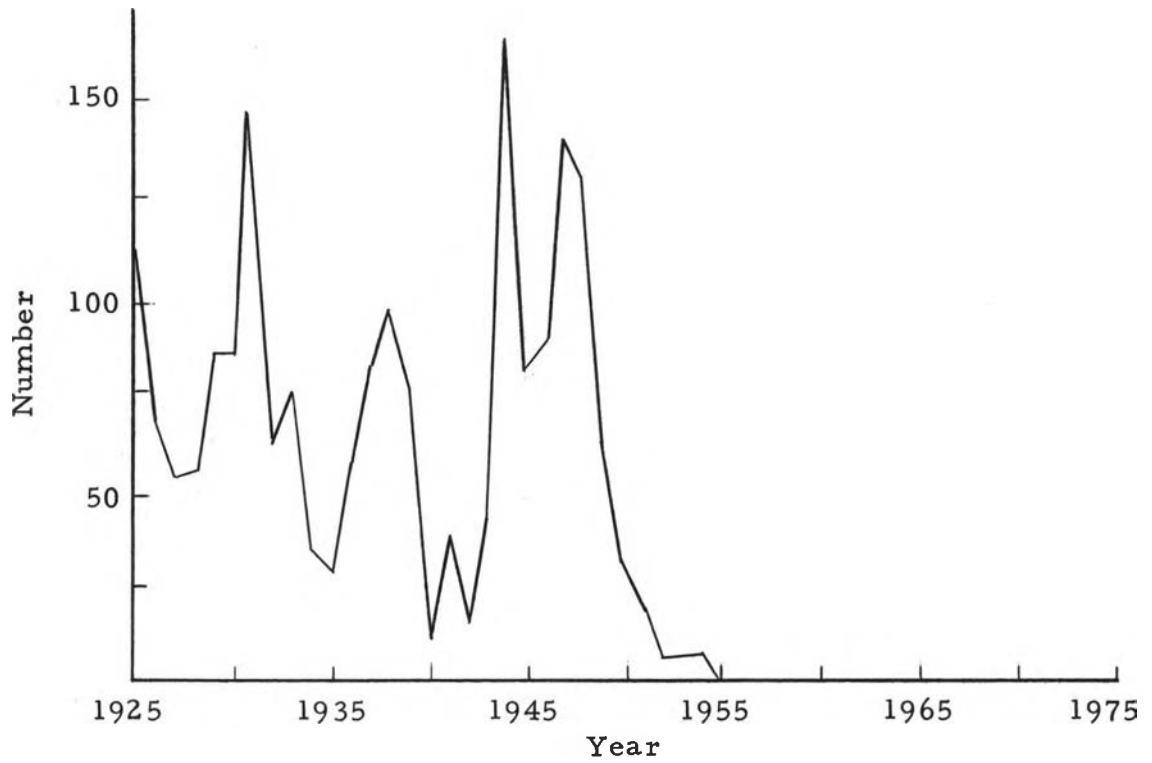
Figure 12. Number of coyotes removed from the Wichita Mountains
Wildlife Refuge during predator-control operations.

region, precipitation decreased east-to-west as did deer densities.
Regarding the relation between precipitation and deer numbers, Teer
et al (1965:22) believed densities of deer in the area were related to
mean annual precipitation of the preceding year. They found the
relation closest during years of drought.

Precipitation records for the refuge reveal below-average
precipitation beginning in 1963 and continuing uninterrupted for 5
years (Fig. 13). Only 4 of the 11 years 1963 through 1973 received
precipitation amounts at or above the long-term average. The
interesting point is that the decline in recruitment in the deer herd
apparently started at about the same time as did the onset of low
precipitation amounts, possibly suggesting a cause-and-effect rela-
tionship.

A range survey made in spring 1966, 3 years into the drought,
showed production of range herbage 50 percent below normal
(Kingery 1966). Regarding food conditions for deer, the report con-
cluded "Browse conditions, particularly for deer, have continued to
decline. Under drought conditions, competition between grazing
species for the limited green forage is intense."

Reproduction and mortality are both known to be affected by
food supply. Verme (1969) experimented with the impact of nutrition
on reproduction by white-tailed deer and found decreases for both
yearling and prime age females receiving inadequate diets. The
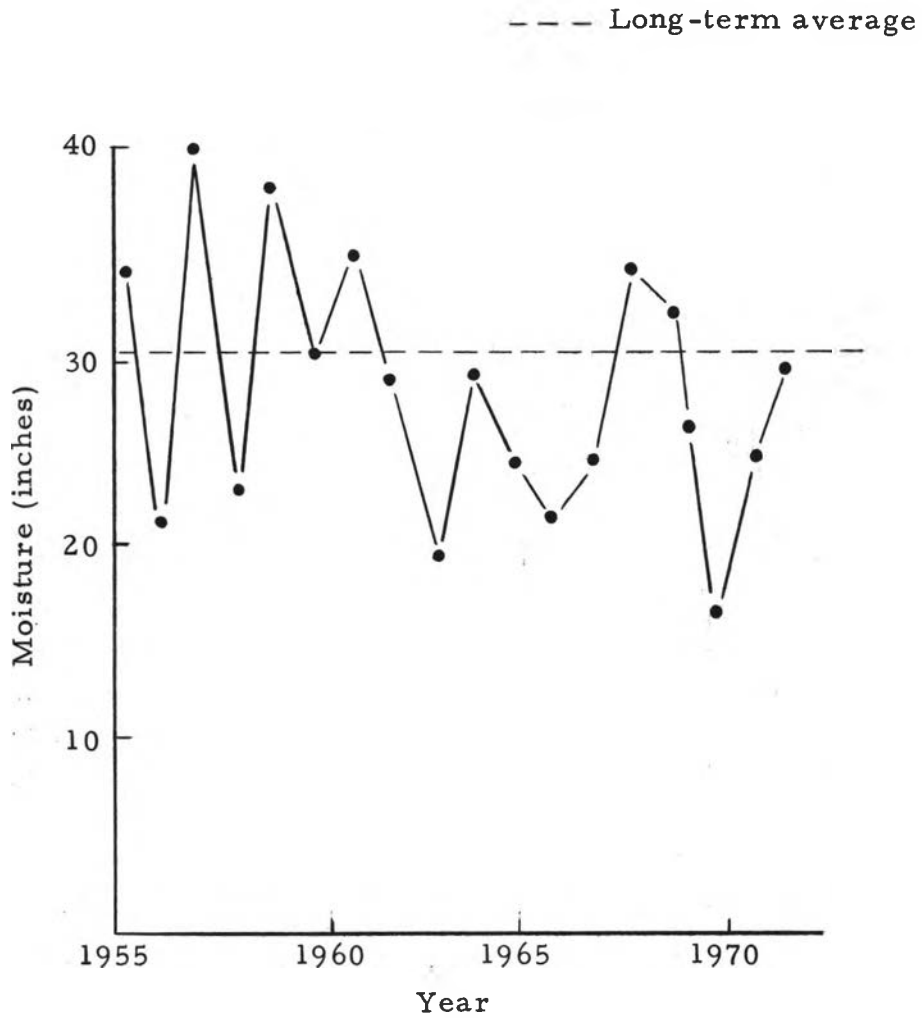
Figure 13. Total amount of moisture received annually on the Wichita Mountains Wildlife Refuge between 1955 and 1972. Long-term average is for the period 1906-1955.

average number of fawns per yearling doe decreased from 1.63 on maintenance rations to only 0.62 fawns per doe (-62 percent) on sub-maintenance diets. Among prime-age females, reproduction decreased from 1.80 to 1.36 fawns per doe (-24 percent).

Teer et al (1965) found that mortality rates increased under drought conditions, starvation being the major cause of death. During 1954 and 1956, when rainfall was less than half the average and rangelands were in poor condition, losses in the Llano Basin herd amounted to 52 and 28 percent respectively, compared to an average of 16 percent.

Drought cannot be shown to be the sole factor behind the deer decline in Comanche County. But events on the Wichita refuge plus the findings about the impact of drought reported by other workers demonstrate that drought was an important contributing factor.

Disease and Parasites. Little has been reported about the incidence of disease and parasites for deer on the refuge. Steele (1969) examined 127 deer taken in the area between 1966 and 1967, finding minimal occurrences of either disease or parasites. One parasite isolated and identified was the fringed tapeworm (Thysanosoma actinioides), a common inhabitant of deer gastro-intestinal tracts according to Herman (1945).

Ticks might have been one source of deer mortality during the 1960's. Bolte et al (1970), working in southern Oklahoma, reported

17 percent of the white-tailed deer fawns they examined during June and July of 1968 and 1969 had infestations of lone star ticks (Amblyomma americanum) extensive enough to cause death. They projected that 34 percent of the 1968 fawn crop was lost to tick mortality. During that same time period, ranchers in the vicinity of the refuge reported finding dead deer having engorged ticks about the head, neck and chest (Steele 1969). The ticks could not be identified as the cause of death, however. Deer passing through check stations in Comanche County between 1965 and 1967 likewise had infestations of various ectoparasites but Steele judged them insufficient to cause death.

Reliability and Completeness of Field Data

The final step in the synthesis of data for the Wichita herds was to assign numerical ratings to the field data for each species which reflected the overall reliability and completeness of those data. The rankings in turn played an important role in deciding how to adjust or "calibrate" the parameters in the simulation model when errors in the synthesized field data were detected.

Table 13 contains a listing of the more important demographic variables required to simulate a herd's history with Program ONEPOP. Each variable in the table has been rated on a scale of 1 to 10, reflecting what appears to be the overall accuracy of that

Table 13. Relative reliability and completeness of demographic information for big game species on the Wichita Mountains Wildlife Refuge. See text for explanation of rankings.

Demographic Variable	Longhorn Cattle	Bison	Elk**	White-tailed Deer
A. Population Information				
Population size	10	10	4	2
Population trend	10	8	9	9
Herd sex structure	8	8	4	4
Herd age structure	8	8	4	4
B. Reproductive Information				
Minimum breeding age	9	8	8	3
Age specific natality rates	4	5	6	2
Total calf crop (or calf:cow ratio)	9	9	3	4
Sex ratio of the calf crop	8	7	3	2
C. Harvest Information				
Total harvest (or harvest rate)	10	10	9	9
Sex structure of the harvest	2	2	8	8
Age structure of the harvest	2	2	5	8
Time of year harvest occurs	9	8	9	9

Table 13. Continued.

Demographic Variable	Longhorn Cattle	Bison	Elk	White-tailed Deer
D. Mortality Information				
Sex-specific mortality rates	5	4	3	1
Age-specific mortality rates	5	2	3	3
Time of years mortality occurs	2	1	3	3
Wounding losses	10	9	6	8
Total annual mortality	6	6	3	1
Average Ranking	6.9	6.3	5.3	4.7

[**]Rankings refer to field data compiled prior to 1969.

piece of field data as being representative of the true population value. A low numerical ranking indicates little confidence in the information whereas higher numerical rankings indicate that the quantity and quality of the data are believed to be good. It should be emphasized that the rankings are subjective and largely reflect the volume of data for each variable found recorded in various refuge documents plus consideration given to how the field data were obtained. For example, information on longhorn herd size was considered to be excellent because it has been obtained each year by corraling the entire herd and making direct counts. On the other hand, less confidence was felt in sex- and age-specific natural mortality information because those data have not been compiled for all years.

DEMOGRAPHIC MECHANISMS OF POPULATION CHANGE

Program ONEPOP is essentially a hypothesis, in the form of
mathematical statements, formulated to explain how big game popu-
lations change over time given certain assumptions about prevailing
ecological conditions. Thus, a validation study would be incomplete
if it did not investigate the mechanisms of population change and
Program ONEPOP's compatibility with those mechanisms. This
section outlines what those mechanisms appear to have been for the
Wichita ungulate herds as elucidated from data stored in the refuge
files.

Historical Patterns in Population Trend

Reported population trends for bison and longhorn cattle are
shown in Figs. 14 and 15 respectively. Both herds experienced
rather constant growth rates until the 1950's after which time the
longhorn herd ceased to grow and has been essentially constant. The
bison population, on the other hand, has been more variable since the
1950's with preharvest herd levels fluctuating between 900 and 1200
animals.

White-tailed deer and elk on the Wichita have experienced both
periods during which their reported numbers were relatively constant
as well as periods of rapid population change (Figs. 16 and 17). As
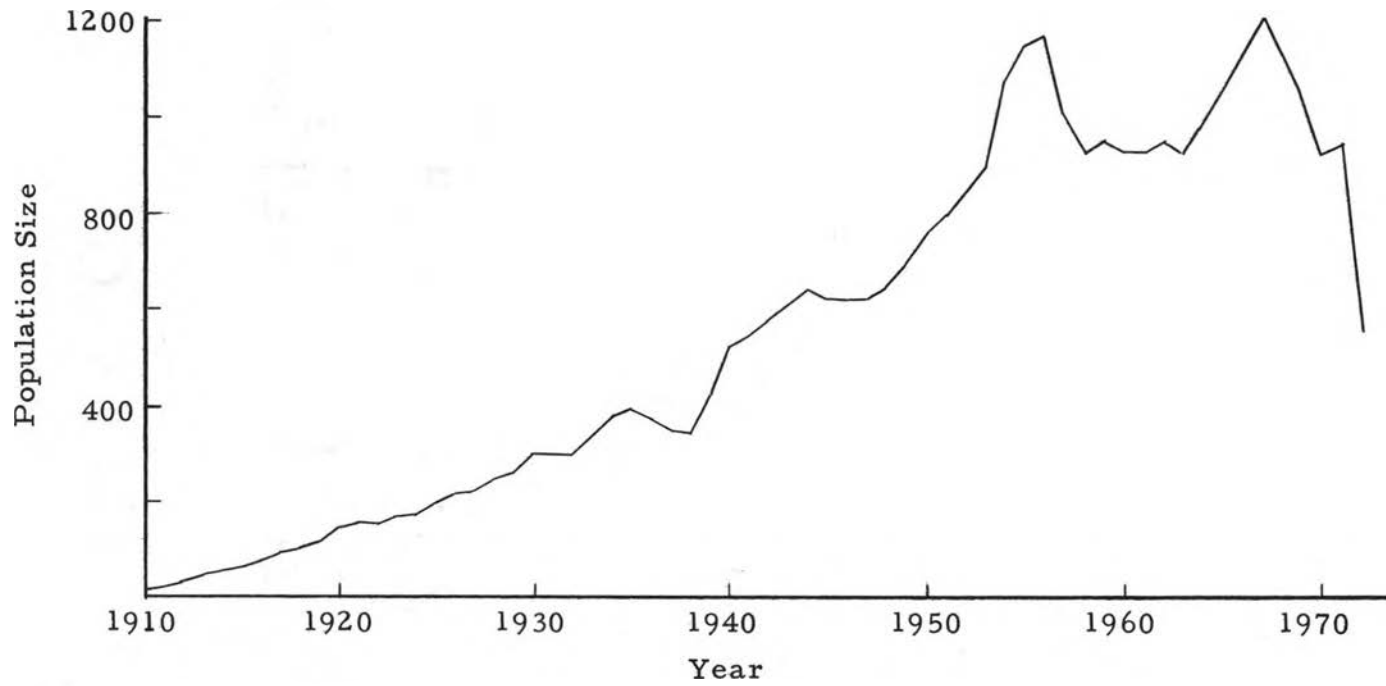
Figure 14. Reported population sizes and trend for bison on the Wichita Mountains Wildlife Refuge.

Figure 15. Reported population sizes and trend for longhorn cattle on the Wichita Mountains Wildlife Refuge.
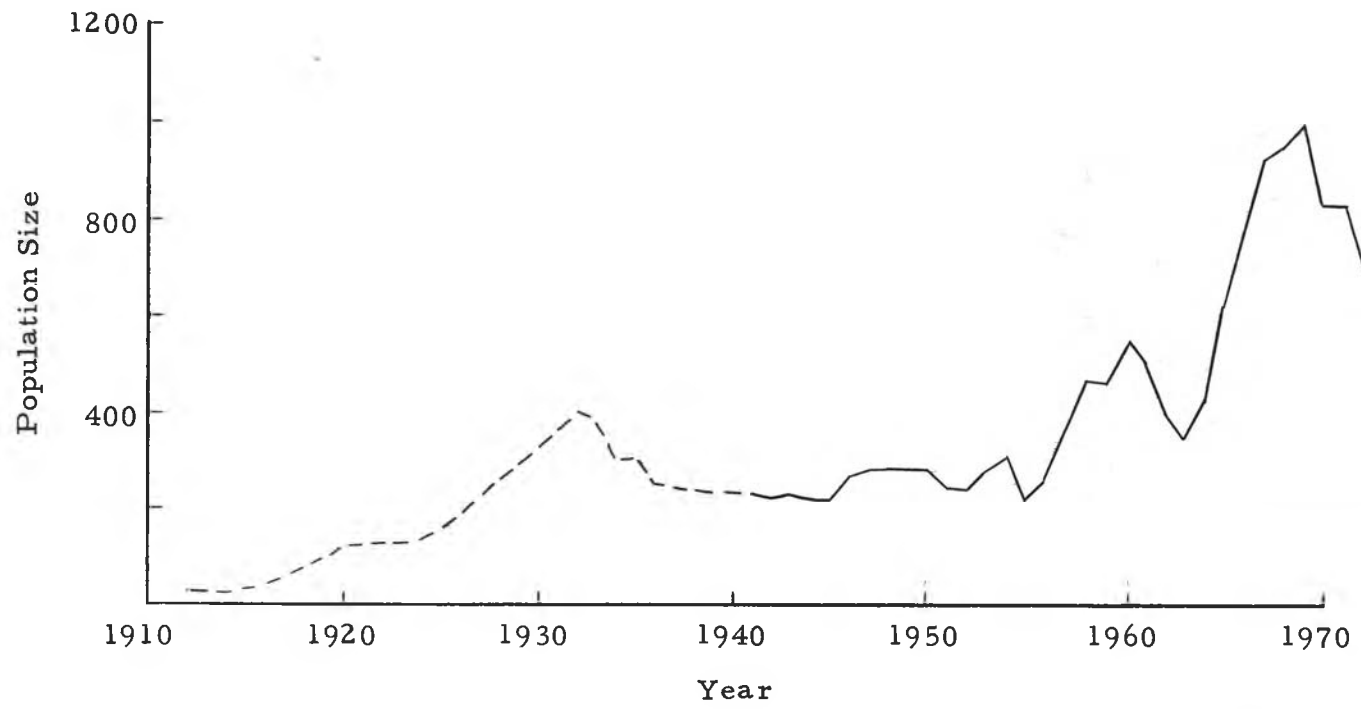
Figure 16. Reported population sizes and trend for elk on the Wichita Mountains Wildlife Refuge. Dotted line depicts suspected values.
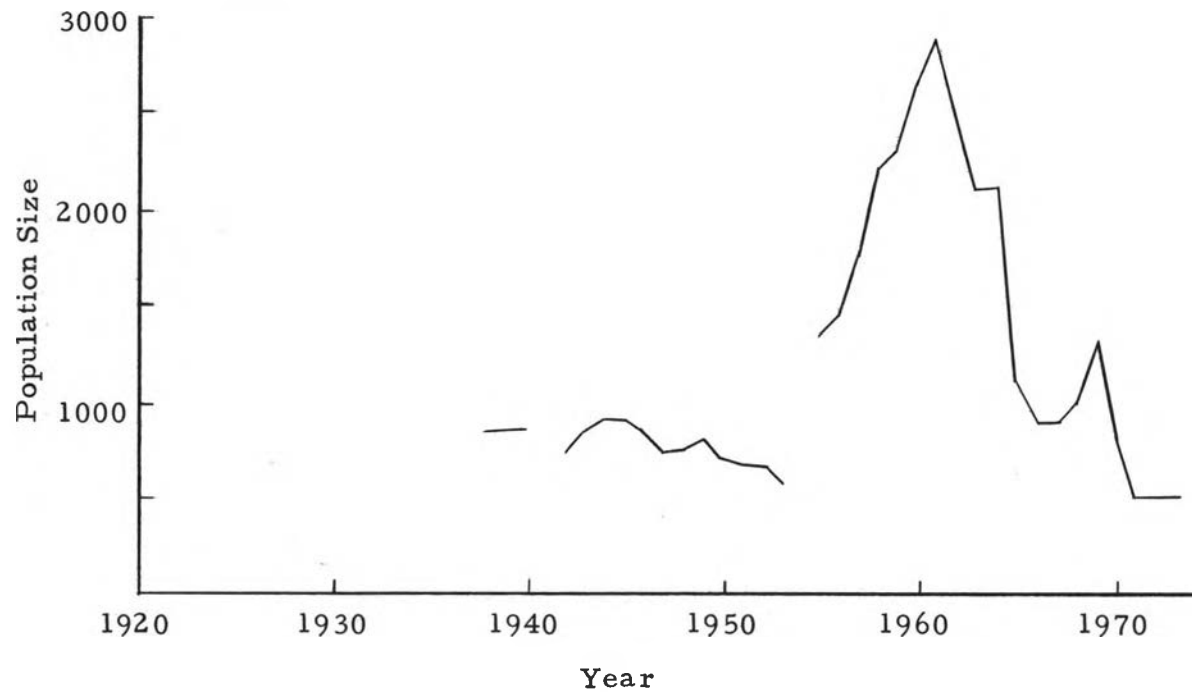
Figure 17. Reported population sizes and trend for white-tailed deer on the Wichita Mountains Wildlife Refuge.

discussed in the preceding section, white-tailed deer increased rapidly in the 1950's and early 1960's only to decline substantially during the late 1960's and early 1970's. Elk also increased greatly in number during the 1960's, attaining a preharvest maximum of nearly 1100 animals. Herd level declined, however, during the late 1960's.

Mechanisms of Population Balance

The population trend described for each herd on the Wichita can be broken down into two components: (1) the average population size over long periods (i.e., the population's mean density) and (2) the year-to-year fluctuation about mean density. These two attributes of population trend may result from the same biological mechanism or they may be caused by entirely different mechanisms. With the exception of white-tailed deer, the refuge staff has adjusted annual harvest tactics over time to attain a desired herd level, i.e., maintain a desired mean density. The chosen mean densities, however, refer to postharvest population size. Still unexplained are the demographic mechanisms or processes through which fluctuations in pre-harvest population size have occurred. These are the mechanisms having most bearing upon annual population yield. Possible factors responsible for such fluctuations include: (1) movements, (2) annual changes in death rates and, (3) annual changes in birth rates.

Movements

Although movements by animals onto and off of the refuge could bring about year-to-year variation in preharvest herd size, this was an unlikely explanation of the variation observed on the Wichita. The 8-foot fence enclosing the refuge is a likely deterrent for animals entering or leaving the area.

Mortality and Reproduction

In order to ascertain whether or not reproductive and mortality variations contributed to annual variation in preharvest population sizes, statistical coefficients of determination (r^2) were computed to quantify the amount of preharvest variation "explained" by selected reproductive and mortality factors. Those factors having highest r^2 values were taken as the most significant contributing factors.

Mortality occurring within the refuge herds was broken down into two components: (1) that resulting from natural causes and (2) that resulting from harvest. Although many longhorn cattle and bison were disposed of alive, those reductions were considered as "harvest mortality" for purposes of this paper.

Variations in preharvest population size explained by natural mortality and harvest rate are shown in Table 14. Preharvest population size is an estimated value, calculated by adding the reported harvest to the reported December herd size. Harvest rate was computed as a percentage of the preharvest population and was

Table 14. Results of tests of statistical correlation between esti-
mated preharvest population size and selected population
mechanisms for big game species on the Wichita Moun-
tains Wildlife Refuge.

Mechanism	N	r Value	Level of Significance[1]	r^2 Value
A. Bison				
Harvest Rate	18	-0.698	0.01	0.487
Natural Loss	14	-0.345	N.S.	0.119
Calf Crop	18	0.768	0.01	0.589
B. Longhorn Cattle				
Harvest Rate	18	-0.193	N.S.	0.037
Natural Loss	15	-0.182	N.S.	0.033
Calf Crop	18	0.706	0.01	0.498
C. Elk				
Harvest Rate	18	0.693	0.01	0.480
D. White-tailed deer				
Fawn Crop	16	0.371	N.S.	0.138

[1] Not significant at P = 0.05. Critical values are according to
Rohlf and Sokal (1969).

compared with preharvest population size of the following year whereas natural mortality was expressed as a percentage of the preharvest population size during the year in which the mortality occurred. In essence, this method compressed all natural loss into the period between the first of the year and the time of harvest.

As might be expected, preharvest population sizes of bison and elk were significantly correlated with their respective harvest rates of the previous fall. Harvest rates and preharvest population sizes of longhorn cattle were not, however, significantly correlated at the 5 percent level. Harvest rate was not tested against population trend for white-tailed deer because the herd was harvested only until 1964.

Natural mortality rates were not significantly correlated with preharvest population size at the 5 percent level for either bison or longhorn cattle. Unfortunately, information about natural mortality of elk and white-tailed deer was too fragmentary to permit an assessment of its impact on the preharvest population sizes of those species.

In contrast to natural mortality patterns, significant correlations were found between reproductive crop and preharvest population size at least for bison and longhorn cattle. The proportion of variation in preharvest population size explained by variation in calf crop size was greatest for bison, with nearly 60 percent of the variation being explained. The correlation coefficient computed between fawning rate and preharvest population size of white-tailed deer was

not significant (p = 0.05) but this was thought due to the fact that heavy fawn losses occurred shortly after birth. Fawning rates used in the analysis were calculated from August and September herd counts. Thus, the fawning rate for any given year reflected not only the number of fawns born but also any postnatal mortality which may have occurred from time of birth to September. It would have been meaningless to make similar comparisons for elk since preharvest population estimates were derived from information on calving rate.

The analysis of these data seemed to merit two conclusions regarding the significance of reproduction and mortality in the refuge herds. First, it appeared as though losses due to natural causes played a minor role in the herd dynamics of all species on the refuge, with the exception of white-tailed deer. Natural death rates were not correlated with population sizes and therefore may be said to have been density-independent. On the other hand, it also seemed plausible to conclude that the two factors which did have significant roles in determining preharvest population size were harvest rate and reproductive rate. Naturally harvest rates can be regulated at the discretion of the refuge staff but reproductive rates cannot be controlled. Reproductive rates for populations are determined by a multitude of factors as behavioral and environmental characteristics. Some of the environmental factors which appear to have influenced reproductive rates for the Wichita herds and their mode of action are discussed below.

Factors Contributing to Reproductive Changes

Precipitation

Various methods have been used to evaluate reproduction for
the refuge herds. In some cases, the indicator of reproduction has
been incidence of pregnancy among females examined during fall. In
other situations pregnancy status was not determined but the number
of young produced was measured, either in the form of actual counts
or as young:female ratios. Regardless of the method used, correla-
tions existed between these measures of reproductive performance
and other variables. One such variable was total annual precipitation.

Bison Calving Rates. The best example of the relation between
the amount of moisture received and reproduction was found in bison
calving rates. Fig. 18 compares bison calving rates recorded be-
tween 1918 and 1938 with total annual precipitation of the previous
year. Calving rates recorded after 1938 were not considered in the
analysis because husbandry actions taken on the refuge at that time
also had bearing on calving rates, making it impossible to determine
the variation due solely to precipitation patterns. Likewise, data
recorded prior to 1915 were not considered because the herd was not
well established and calving rates were erratic between years for such
reasons as insufficient number of bulls to breed all cows.

Statistical analyses revealed a significant (p = 0.05) correla-
tion between bison calving rate and total annual precipitation of the
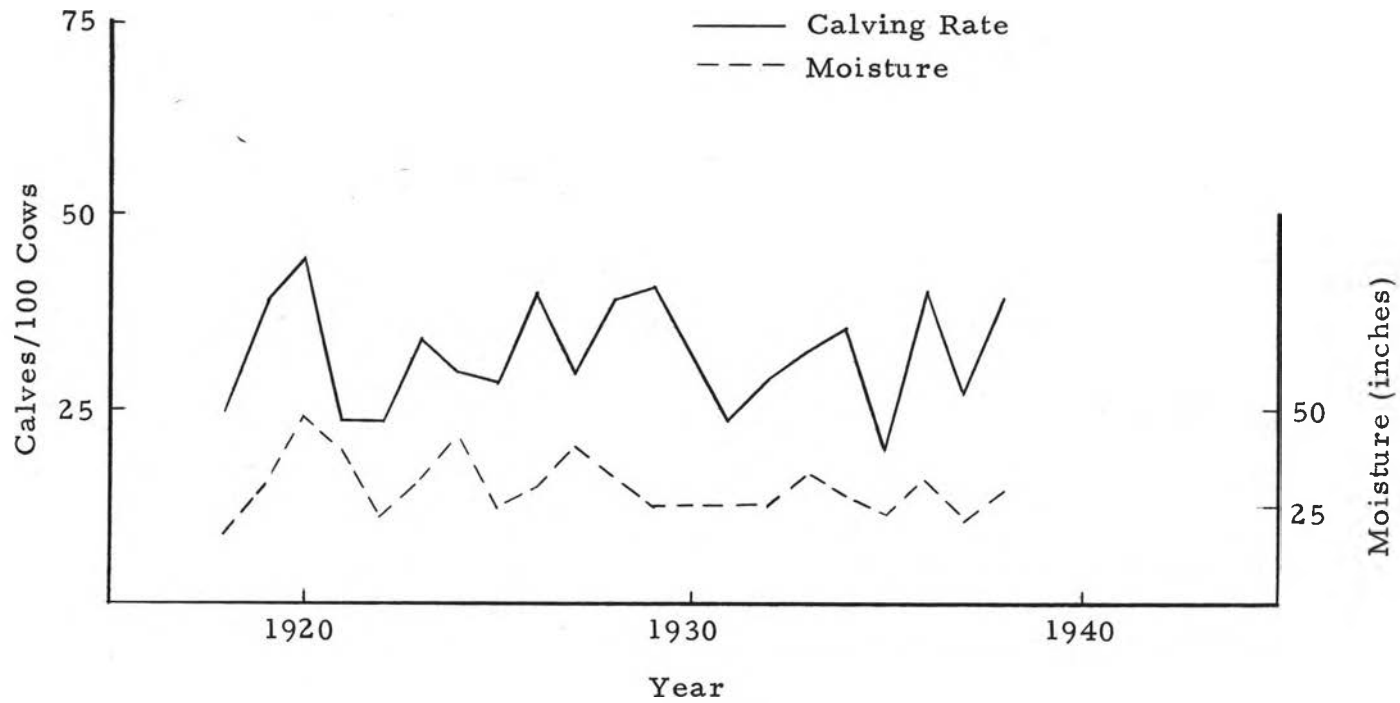
Figure 18. Relation between total annual precipitation and bison calf crop of the following year on the Wichita Mountains Wildlife Refuge.

preceeding year. In general, whenever precipitation amount increased or decreased, bison calving rate the following year did likewise. The fact that the correlation was strong enough to be significant at the 5 percent level may imply a cause-and-effect relationship between the two events.

Incidence of Pregnancy Among Elk. Pregnancy rates recorded for elk during the late 1960's and the early 1970's were also positively correlated with total annual precipitation although the correlation was not statistically significant at the 5 percent level. The pattern noted for elk was similar to that described above for bison calf crops in that incidence of pregnancy among adult elk cows was higher during years receiving higher amounts of moisture (Fig. 19).

An apparent discrepancy occurred in the pattern in 1971 however. Incidence of elk pregnancy observed in the fall of 1971 was the highest recorded during 1969 through 1972. This was in obvious contrast to total annual precipitation for 1971 which was well below the long-term average and the second lowest amount received during the 4-year period. One aspect that made 1971 different from most years was not so much total annual precipitation but rather the seasonal distribution of that moisture. During 1971, 18.7 cm (7.38 in) or about 30 percent of the annual total fell during August and September, immediately before and during the elk rutting period. By comparison, the long-term average amount of moisture for
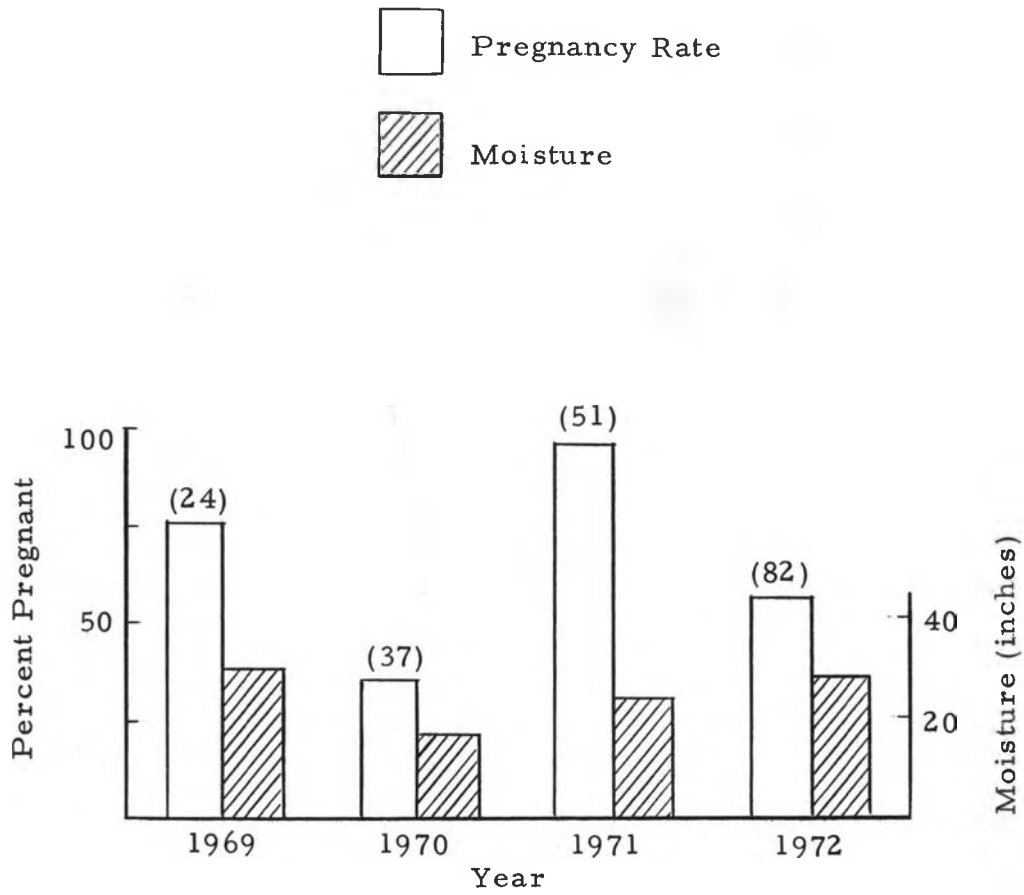
Figure 19. Relation between incidence of pregnancy and total annual precipitation of the same year for elk on the Wichita Mountains Wildlife Refuge. Sample size is shown in parentheses.

August and September was only 13.8 cm (5.43 in) or 18 percent of

the average annual total. Thus, data collected in 1971 strongly

suggested that reproduction by the refuge elk herd was influenced to

a greater extent by August and September moisture totals rather than

by total annual precipitation. This conclusion was further supported

by data collected in 1969, the year having the second highest preg-

nancy percentage for elk during the same 4-year period. During

1969, 23.9 cm (9.41 in) of moisture, again about 30 percent of the

annual total, fell during August and September. Since reproduction

by other species on the refuge also appeared to vary with precipita-

tion patterns, the findings for elk may apply to those species as well.

There existed a close relation between precipitation and range

forage production on the Wichita refuge. In general, forage produc-

tion on the refuge increased or decreased with moisture amount. If

we assume that the heavy August and September rains of 1969 and

1971 stimulated the growth of plant species consumed by elk, the

higher pregnancy incidence noted could be evidence of "flushing"

among Wichita elk. Flushing, the act of feeding female animals a

concentrate of high nutritive value shortly before and during the

breeding period, is a technique used to increase ovulation rates in

domestic animals (Zimmerman et al 1960). According to Moustgaard

(1969:205), lamb production by domestic sheep can be increased 10 to

20 percent by raising the concentrated food intake of ewes a few weeks

prior to breeding. He also stated that the procedure is most effective when ewes are previously maintained on less-than-optimal diets. In this light, it is interesting to note that elk pregnancy rate for 1971 was 70 percent greater than the average for the other three years under consideration. Other investigators have raised the question about flushing in wild ungulate herds as well. For example, Ransom (1967) speculated that a high rate of ova loss among white-tailed deer in Manitoba resulted from an exceptionally high ovulation rate that may have been brought about by conditions analogous to flushing. Likewise, Edwards and Ritcey (1958) believed that their study of moose (Alces alces) in British Columbia dealt with two populations from a nutritional point of view and that conditions similar to flushing were producing higher twining rates in one than the other.

If flushing does occasionally occur in the Wichita elk herd, it seems likely that it must involve a slightly different mechanism than that described above by other workers. The studies cited above all dealt with species capable of giving multiple births. But elk are not known to bear twins on the refuge. Thus, if ovulation among elk is affected by level of nutrition during late summer and early fall, it must be that flushing causes a greater percentage of the herd females to ovulate as opposed to causing each female to produce more ova, thereby increasing the incidence of multiple births as is normally found when flushing takes place. Observations supporting that conclusion are presented below.

Age-Specific Pregnancy Rates for Elk. Reproductive potential is known to vary considerably among age classes of wild ungulates. Ransom (1967) reported that ovulation rates for white-tailed deer in Manitoba were significantly higher among adult does than among fawn and yearling does. Simkin (1965) found similar patterns in moose. Since reproductive potential does vary between age classes, it seemed likely that environmental factors, such as total annual precipitation, which might directly or indirectly influence reproduction in some way, would impact upon age classes in different ways. Pursuant to that speculation, pregnancy data obtained between 1964 and 1973 from butchered elk and also from elk taken by hunters were summarized by age classification and divided into two groups based upon total annual moisture of the year during which the observations were made. Data collected during years in which total annual moisture equaled or exceeded 28 in (71 cm) were considered typical of "wet" years whereas data collected during years receiving lesser amounts of moisture were considered typical of "dry" years.

Chi-square analyses revealed that significantly ($X^2 = 29.5$, n = 2, p = 0.01) greater numbers of 2-year-old cow elk were pregnant during wet years than dry ones. Incidence of pregnancy for 2-year-old cows varied from 2.8 to 58.8 percent between dry and wet years respectively whereas incidence of pregnancy among adult cows was more consistent between wet and dry years (Table 15).

Table 15. Comparison of pregnancy rates for elk according to age
and moisture conditions on the Wichita Mountains Wildlife
Refuge. (Percentages are given in parentheses.)

Type of[1] Year	Age		Totals
	2 Yrs.	3^+ Yrs.	
Wet	$\frac{10}{17}$(58.8)	$\frac{157}{232}$(67.7)	$\frac{167}{249}$(67.1)
Dry	$\frac{1}{35}$(2.8)	$\frac{244}{386}$(63.2)	$\frac{245}{421}$(58.2)

[1]Wet years were 1964, 1969, 1972 and 1973.
Dry years were 1965, 1966, 1967 and 1970.

Overall herd pregnancy rate was also higher during wet years than during dry years.

With the limited amount of data available, it was impossible to determine if breeding by younger cows was primarily responsible for the variability observed in elk calving rates over time. For example, during 1972, when elk calving rate exceeded 70 percent, only one 2-year-old cow had been examined during the previous fall and she was not visibly pregnant. On the other hand, 8 of 12 (67 percent) 3-year-old cows shot during 1972 were lactating, indicating they had produced a calf in 1972 and, therefore bred in 1971 as 2-year-olds. It was also interesting to note that one of twelve $1\frac{1}{2}$-year-old cows examined during 1972 was pregnant (Bartnicki 1971). Such observations added to the speculation that breeding by younger cows was an important element in the year-to-year fluctuations observed in elk reproduction on the Wichita. More intensive efforts should be undertaken to document the relations between August-September moisture, reproduction by yearling females, and herd calf crop sizes.

White-tailed Deer Fawning Rates. Fawning rates for white-tailed deer on the refuge appeared also to be somewhat related to precipitation. There was a general tendency for fawn production to increase during years following an increase in total annual moisture, as well as vice versa, between the mid-1950's and the early 1960's although the relation apparently reversed itself after 1963 (Fig. 20).
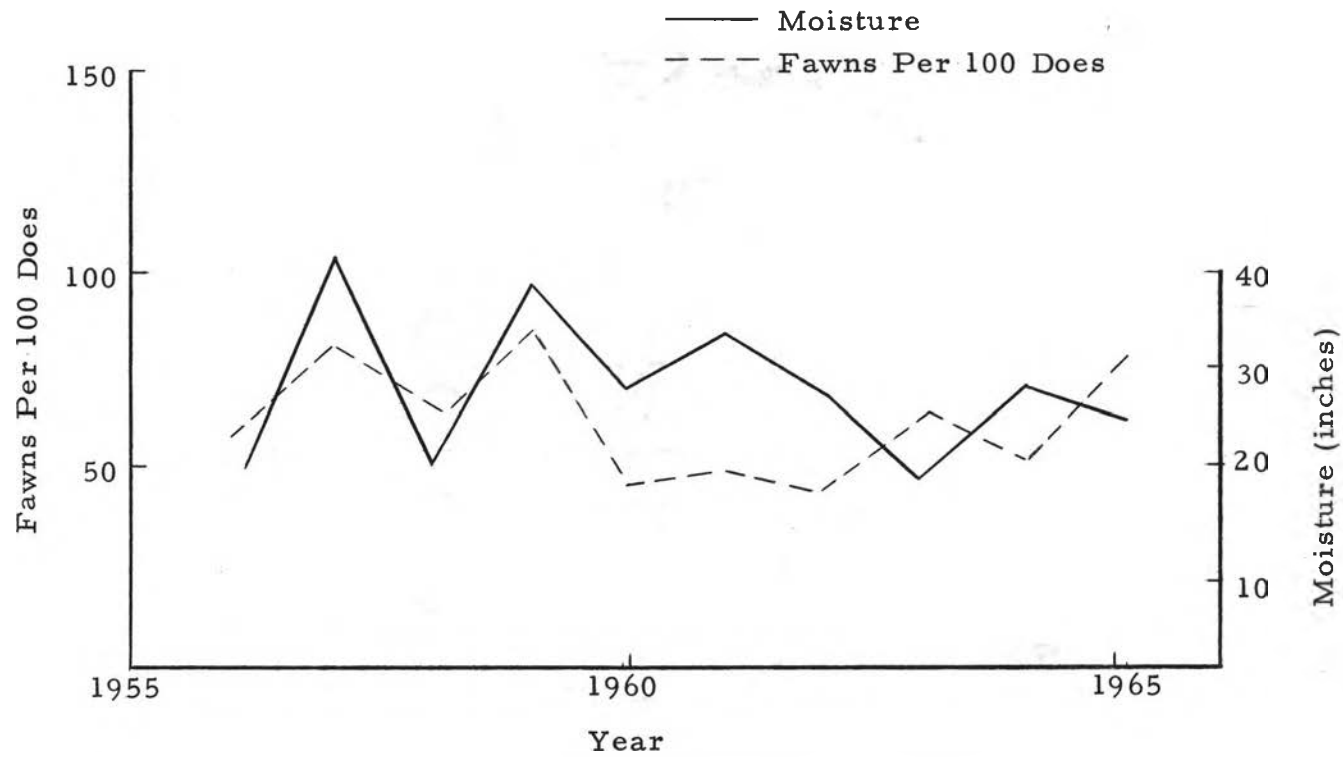
Figure 20. Relation between fawning rate for white-tailed deer and total annual moisture recorded during the previous year on the Wichita Mountains Wildlife Refuge.

The correlation between fawns per 100 does and total annual precipitation was not significant at the 5 percent level. But the statement made by Teer et al (1965:22) that deer numbers in the Llano Basin were related to precipitation patterns of the preceding year implied a delayed response between precipitation and deer numbers. That delay would be explained if the influence of precipitation was somehow exerted by means of reproduction.

Forage Production

The hypothesis was advanced above that heavy rains during August and September of 1969 and 1971 stimulated forage production in the Wichita Mountains region. It was further hypothesized that that increase in forage production brought about better nutritional conditions immediately prior to and during the elk rut and accounted for the unusually high incidence of pregnancy among elk shot by hunters during the fall of those years. In order to additionally test the hypothesis that reproductive performance of refuge ungulates was closely linked to forage production and range trend, correlation tests were made to compare calving rates of bison and elk with forage production in the areas frequented by those species. Longhorn cattle were excluded from all analyses of reproductive variation because of the artificial manner of which longhorn reproduction has been controlled on the refuge. Data for white-tailed deer were generally too fragmentary to permit a quantitative analysis.

Elk Pregnancy Rates. Elk pregnancy rates recorded between 1969 and 1972 were not significantly correlated with estimates of forage production during the same time span. The correlation became significant ($r = 0.995$, $p = 0.01$), however, if the data for 1971 were dropped from the test. The proportionate increase in elk pregnancy rate between 1970 and 1971 was much larger than the corresponding increase in forage production (Table 16). As noted above, this may have reflected the heavy August and September rains and subsequent flushing in the elk herd.

Bison Pregnancy Rates. Comparisons between estimated forage production and pregnancy rates for bison are presented in Table 17. There was no significant correlation ($r = 0.773$, $p = 0.05$) between the two variables but they did at least exhibit similar trends over time. Both forage production and bison pregnancy rates declined throughout much of the 1960's. The decline in forage production was believed due to the drought conditions which occurred during the same time interval. The decline in bison pregnancy rates is perhaps a reflection of the declining forage production.

Lactation Status

At the time of the fall elk hunt, individual cows were examined for pregnancy status and also to determine whether or not they were lactating. If a female was lactating, it implied that she was still nursing a calf born during the previous calving period. Thus,

Table 16. Comparison between average forage production on
          Boulder Ridge and Hilly-Stony range sites and elk
          pregnancy rate, Wichita Mountains Wildlife Refuge.

Year	Estimated Forage Production (Pounds/Acre)	Pregnancy Rate
1969	2395	75
1970	1243	32
1971	1839	92
1972	2302	55

Table 17. Comparison between average forage production on Loamy
          Bottomland range sites and pregnancy level in adult (3^+
          yrs.) bison cows, Wichita Mountains Wildlife Refuge.

Year	Estimated Forage Production (Pounds/Acre)	Pregnancy Rate
1961	6500	--
1962	5350	--
1963	---	82
1964	4392	80
1965	2312	71
1966	3758	71
1967	2405	69
1968	3873	73

information on the incidence of lactation among cows shot by hunters was an additional means of estimating the calf crop percentage. In essence then, three independent estimates were made to calculate elk reproduction during any given year: (1) pregnancy rate in December, (2) calf:cow ratio in August and September, and finally (3) lactation rate during December following the birth of the calves.

Data obtained on the lactation status of adult cow elk during recent years suggested an inverse relationship existed between lactation and pregnancy among elk on the Wichita. Correlation tests run on lactation and pregnancy data collected between 1969 and 1973 indicated that the two variables were negatively correlated although not significantly ($r = -0.223$, $p = 0.05$). The pattern over time (Fig. 21) was one of rather high incidence of pregnancy and low incidence of lactation in one year followed by the inverse relationship the next year. If the relationship is real, it would indicate that cow elk, on the average, did not conceive calves while still nursing the current year's calf. The net result would be that cows would produce off-spring in alternating years.

The above pattern noted for elk was similar in certain respects to that described for bison in a previous section of this paper. Although lactation data were not available for bison, a tendency for bison cows to bear calves in alternating years was observed during the early 1960's. It seemed conceivable that similar biological mechanisms could be operating in both populations.
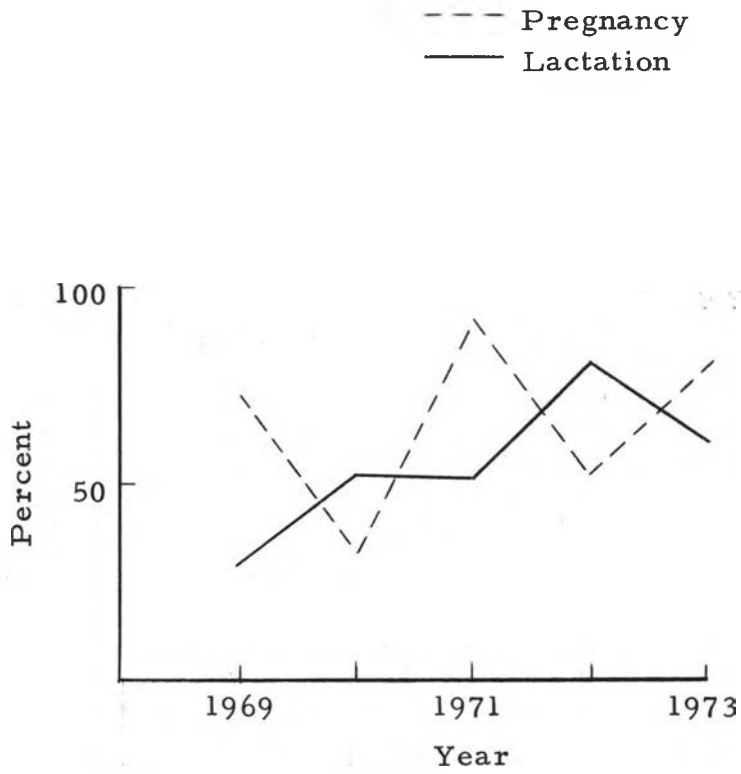
Figure 21.   Relation between lactation and pregnancy rates for mature
cow elk on the Wichita Mountains Wildlife Refuge.

Discussion

Interpretation of Results

The data dealing with reproduction and related variables sum-
marized and subjected to statistical evaluation above are, admittedly,
often fragmentary and incomplete. In some cases the quality of the
information must be suspect. However, taken as a whole, the rela-
tions pointed out above do seem convincing enough to permit some
basic generalizations about the Wichita grazing system.

First, it seems evident that the data gathered on the Wichita
support the already widely-held belief that range condition has a
strong bearing upon ungulate reproduction. Reproduction by some of
the refuge herds was correlated with precipitation patterns and, in a
few cases, the correlations were strong enough to demonstrate
statistical significance. The most logical mechanism through which
precipitation patterns could have a consistent impact upon ungulate
reproduction would be via range condition.

There also appears to be support for Verme's (1969) findings
that nutritional conditions at time of breeding are an important factor
affecting reproduction by wild ungulates. On the Wichita at least, it
appeared that nutritional conditions at that time of year were all
important because they determine the herd's reproductive potential,
at least for that particular year. Any decrease in that potential must
have been due to conditions, nutritional or otherwise, existing during

the winter months and also during the spring, immediately prior to birth. Data available from the Wichita did not lend themselves to an analysis of conditions during that period. Therefore, it was impossible to determine from this study how winter and early spring nutritional conditions might affect herd reproduction.

The pattern between pregnancy and lactation rates for elk discussed above could be an indication of how energy requirements of the animal and reproduction are interrelated in a wild population. Studies carried out with domestic animals have shown that lactation places heavy demands upon the energy expenditure of those animals. Morrison (1950:222) stated that metabolic rate, as measured by heat production in the body, is twice as high in lactating animals as in those which are not yielding milk. Maynard and Loosli (1969:469) summarized the energy-balance studies carried out on dairy cattle by several investigators with the conclusion that the average utilization of metabolizable energy for milk production was 69.3 percent. This would imply that only slightly more than 30 percent of all metabolizable energy is available for such other needs as body maintenance, heat increment, growth, travel and production of a new fetus.

Elk are known to nurse their calves long after the rutting period. Bartnicki (1971) even concluded that some yearling elk on the Wichita nurse their mothers. Assuming energy partitioning in

elk is similar to that described for dairy cows, the inverse relation-
ship between lactation rate and pregnancy rate could have been caused
by a situation in which energy availability during the fall rut was inade-
quate to meet the demands of both lactation and ovulation, the end
result being a low incidence of ovulation in the herd and consequently,
low pregnancy rate. The inverse condition could easily have occurred
the following year since by that time most cows would have weaned
their calves and would not be using large quantities of metabolizable
energy to meet the demands of lactation.

Components of the Reproductive Process

From the results and discussion presented above, it was evident
that the reproductive process, as it occurs among wild ungulates, is
complex. Many separate factors, each capable of changing from one
year to the next, act and interact to determine the number of young
produced by the population. In light of this complexity, it seems
almost futile to attempt an assessment of reproduction on the basis of
individual pieces of information such as range condition or population
level. Such approaches may yield reasonable approximations of
reproduction but the predicted value is almost certain to differ from
the true reproduction.

Perhaps a more reliable approach would be to develop a simu-
lation model of the reproductive process. With such a device, several
pieces of relevant information could be integrated to arrive at the

reproductive estimate. Holling (1966) described a procedure, called experimental components analysis, for building models of complex, ecological processes. Basically, Holling's approach resolves any given ecological process into two sets of components -- basic components which occur in all manifestations of the process and subsidary components which are present in some situations and not others. Holling's procedure is to first identify the basic components and their interactions. A computer model is built to integrate these basic components and is then tested against real-world occurrences of the process to evaluate the model's realism. Additional complexity is added as new information becomes available from field experiments.

The basic components and their interactions which seem to be most influential on ungulate reproduction as made evident from study of the Wichita herds are shown in Fig. 22. The items of the conceptual model relate entirely to nutrition (i.e., energy partitioning) and take into consideration only the period corresponding roughly with that between parturition and conception. No doubt many important variables have been omitted. For example, several minerals and vitamins are known to be important for reproduction (Maynard and Loosli 1969). Again, however, the model is not intended to be exhaustive but rather a reasonable place to begin.
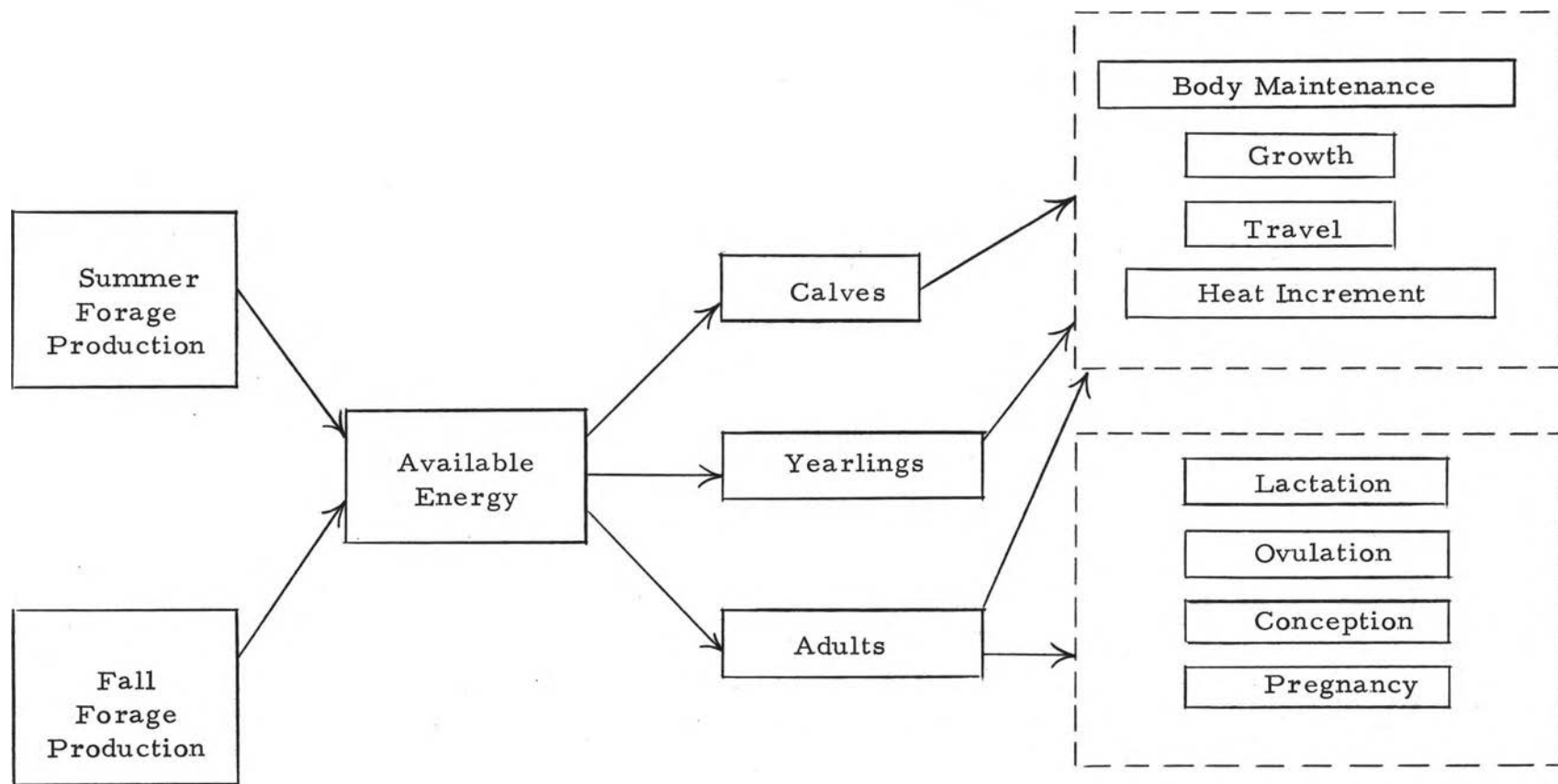
Figure 22. Flow chart showing how energy partitioning appears to affect the reproductive process of ungulates on the Wichita Mountains Wildlife Refuge.

The model is believed to contain the minimum components which need to be taken into account before successful attempts can be made to accurately forecast reproduction in wild ungulate herds. In order to add more realism and precision to the model, each basic component could almost certainly be broken down into several sub-components. These might be additional basic sub-components or they might be subsidary sub-components. To illustrate, the basic component "available energy" might be broken down into sub-components of dietary overlap between sympatric species, foraging limitations and, perhaps, forage palatability. Others might be included as well, all of which act and interact to influence the amount of available energy.

SIMULATION STRATEGIES AND RESULTS

Having described the general population biology of each herd on the Wichita and some of the demographic mechanisms apparently involved in population changes over time, information has now been compiled with which to test Program ONEPOP's ability to reproduce the dynamics of the Wichita herds over time. This section discusses the precision and realism with which Program ONEPOP simulated the Wichita populations as well as the stretegies used to approximate missing or incorrect field data. Some tentative explanations for the differences between reported and simulated values are also offered.

Longhorn Cattle Simulations

Although the data base for longhorn cattle on the Wichita is comparatively good, there are deficiencies and omissions. For example, the total number of animals removed from the herd annually has been recorded throughout the herd's history. But almost entirely missing from the record are data on the sex and age distribution of the annual removals. Information of that nature dates back only to the mid-1960's and thus had to be approximated for all other years in order to simulate population history. Harvest sex ratios were approximated by considering how the reported herd sex and age structure changed from one year to the next.

Information about the sex and age structure of a population is a powerful diagnostic aid in efforts to develop an understanding of the demographic processes operating within that population. In harvested populations (as the Wichita longhorn herd), a disproportionate number of adult males and females in the herd is reason to suspect that there have been unequal numbers of males and females harvested from the herd. The evidence does not constitute infallible proof of disproportionate male and female harvests because an unequal number of adult males and females in the population could also be the result of (1) unequal natural mortality between males and females and/or (2) unequal numbers of males and females recruited into the population through reproduction.

But information reported for the Wichita longhorn population suggested annual changes in herd sex and age structure were probably harvest related. For one thing, there was little evidence of disproportionate mortality between sexes. Nor was there strong evidence that changing herd sex structures were due to unequal male and female recruitment into the population. Of 841 calves born on the refuge between 1927 and 1972, 424 (50 percent) were males and 417 (50 percent) were females. Granted the number of males and females born each year was not exactly equal. But, the differences in the number of male and female calves born in any given year did not seem large enough to account for the difference in the reported

number of male and female adults in the population during the
following year.

In light of these findings and conclusions about longhorn repro-
ductive and natural mortality trends, changes in the sex structure of
the herd from year-to-year probably reflected changes in the number
of males and females removed through harvest. Therefore, since
the total number of animals harvested each year was accurately
known, the annual harvested total was divided between males and
females so as to approximate the reported postharvest sex ratio
which, like total annual harvest, was also considered to be reliable
information.

Longhorn Cattle Simulation Results
1928 Through 1954

Following synthesis, population information obtained from
refuge documents was input into Program ONEPOP in an effort to
reproduce herd dynamics over time. Data adjustments were not
made in the initial simulation; input was exactly as synthesized
above. In some respects, the first simulation represented a "trial
balloon" simulation because, from that initial effort, an assessment
was obtained of how correctly information had been synthesized from
reported field data. If, for example, the simulation failed to
approximate even one or two years of herd history, evidence would
be at hand that major errors had been made in data input, indicating

either (1) the reported information had been compiled and synthesized

incorrectly or (2) the reported field data were not correct. If, on

the other hand, the simulation closely approximated several years

of herd history, it would seem reasonable to conclude data-input

errors had not been made.

Population sizes and trend generated by the initial longhorn

simulation are compared with reported values in Fig. 23. Simulated

output approximated population sizes reported during 1928 through

1945 so closely that, for some years, reported and simulated values

were virtually identical. But reported and simulated population

trends diverged after 1945 when simulated population sizes dropped

consistently below corresponding reported population sizes.

The fact that the simulated population dropped below the actual

population during the late 1940's suggested that synthesized informa-

tion used in the simulation could be wrong in one of several possible

ways. First, the reproductive rates used in the simulation might

have caused the simulated population to decline by producing smaller

calf crops than those in the actual population. Simulated calf crops

lower than those occurring in the actual population would cause the

simulated population to decline if the total number of animals re-

moved each year (harvest plus natural losses) exceeded the number

added through reproduction. Second, essentially the same result

would occur if the simulated mortality rates were greater than those

Figure 23. Comparison of reported and simulated population trend for longhorn cattle on the Wichita Mountains Wildlife Refuge obtained in the first simulation effort.

occurring in the real-world population. Excessive natural mortality would cause the simulated population to decline if net recruitment (births minus natural deaths) did not equal or exceed the number of animals harvested each year. A third possible explanation for the declining simulated population was that the simulated reproductive and mortality rates were accurate but the total number of animals removed through simulated harvest exceeded the actual harvest.

Of the possible explanations for the simulated population decline, errors in reproductive-rate synthesis seemed most likely based upon the following logic. The number of animals removed through simulated harvest was exactly the reported harvest and, since total annual harvest was among the best (most reliable) pieces of field data, it seemed improbable that more animals were harvested during simulation than what had been actually removed. It also seemed unlikely that mortality rates used in the simulation were excessive and to blame for the simulated population decline. The simulated mortality rate (3 percent annually) approximated the reported long-term average mortality level and the fact that the refuge staff corraled and counted the entire herd each year would lower the probability of them making serious errors in estimating the magnitude of natural losses.

With reproductive information being the only remaining variable and therefore the most likely source of error, attention was

focused upon the alignment between reported and simulated values for (1) the number of calves per 100 cows and (2) the number of breeding-age females in the population. If the simulated values for either of those reproductive parameters were lower than the actual values, recruitment into the simulated population would be less than that of the real population, possible accounting for the simulated population decline after 1945.

Inspection of the alignment for longhorn reproductive parameters, shown in Table 18, revealed that the simulated number of calves per 100 cows aligned rather well with reported calving rates through 1943, but that they were consistently lower than actual calving rates reported after that date. A second manner in which the two populations did not align was with respect to the number of cows (females age class 2^+) remaining in the herd immediately after the fall harvest. As also shown by the comparisons in Table 18, there were, with only few exceptions, fewer cows postharvest in the simulated population than there were in the real population during all years simulated. The comparisons indicated that the simulated population declined because there were too few reproducing females in the population and that those which were present, reproduced at a rate below that of the actual population after 1943. The total number of calves produced annually in the simulation was insufficient to replace the annual loss (harvest plus natural mortality), thereby causing the population to decline.

Table 18. Comparison of reported and simulated values (first simulation attempt) for reproductive parameters for longhorn cattle, Wichita Mountains Wildlife Refuge. (Simulated values are in parentheses.)

Year	Calf Crop	Calves Per 100 Cows	Cows Postharvest
1928	14 (11)	74 --	25 (24)
1929	16 (14)	64 (62)	32 (28)
1930	21 (17)	65 (61)	40 (34)
1931	26 (20)	65 (60)	44 (35)
1932	22 (20)	50 (59)	53 (42)
1933	28 (24)	53 (59)	47 (43)
1934	36 (24)	77 (57)	40 (37)
1935	20 (21)	50 (57)	46 (42)
1936	19 (24)	41 (58)	44 (50)
1937	22 (28)	50 (57)	42 (50)
1938	22 (27)	52 (55)	52 (56)
1939	27 (31)	52 (55)	65 (67)
1940	33 (36)	51 (54)	80 (77)
1941	41 (40)	51 (52)	91 (87)
1942	52 (43)	57 (50)	99 (85)
1943	44 (41)	44 (48)	93 (96)
1944	51 (46)	54 (49)	108 (98)
1945	58 (45)	54 (46)	113 (85)
1946	61 (39)	54 (46)	111 (83)
1947	63 (39)	57 (48)	97 (71)
1948	69 (33)	71 (48)	103 (51)
1949	72 (26)	70 (50)	87 (34)
1950	63 (18)	72 (54)	91 (17)

It was pointed out above that sex composition of the annual longhorn harvest was unreported (prior to the 1960's) and that the number of cows removed annually was approximated from information reported on postharvest sex structure. The poor alignment between reported and simulated numbers of cows postharvest indicated that the total annual harvest was probably correct but that preliminary estimates of harvest sex structure caused too many cows to be harvested during most years. Therefore, the number of longhorn females included in each annual harvest was adjusted so that the simulated number of cows postharvest more-closely approximated the reported number. Making those adjustments aligned the number of cows postharvest as shown in Table 19 but simulated population trend still dropped below the reported population trend, similar to the simulation trend described earlier in connection with Fig. 23.

At this point in the analysis, the simulated and real populations were aligned with respect to (1) total annual harvest, (2) average annual mortality, (3) postharvest sex ratio and (4) population size and trend through 1945. The two populations were not aligned with respect to (5) calf:cow ratios after 1943 and (6) population size and trend after 1945. It appeared that better alignment between reported and simulated population size and trend could be obtained by aligning calf:cow ratios in the two populations. Therefore, the reproductive function originally synthesized from the reported field data for the period 1945

Table 19. Alignment of reported and simulated reproductive parameters for longhorn cattle on the Wichita Mountains Wildlife Refuge after adjustments were made in the number of cows harvested annually. (Simulated values are in parentheses.)

Year	Calf Crop	Calves Per 100 Cows	Cows Postharvest
1928	14 (11)	74 --	25 (24)
1929	16 (14)	64 (62)	32 (28)
1930	21 (19)	65 (61)	40 (38)
1931	26 (24)	65 (60)	44 (40)
1932	22 (21)	50 (59)	53 (49)
1933	28 (27)	53 (59)	47 (50)
1934	36 (26)	77 (57)	40 (41)
1935	20 (21)	50 (57)	46 (44)
1936	19 (17)	41 (58)	44 (44)
1937	22 (25)	50 (57)	42 (44)
1938	22 (20)	52 (55)	52 (49)
1939	27 (32)	52 (55)	65 (62)
1940	33 (36)	51 (54)	80 (78)
1941	41 (40)	51 (52)	91 (88)
1942	52 (48)	57 (50)	99 (97)
1943	44 (37)	44 (48)	93 (91)
1944	51 (54)	54 (49)	108 (106)
1945	58 (46)	54 (46)	113 (110)
1946	61 (40)	54 (46)	111 (110)
1947	63 (42)	57 (48)	97 (95)
1948	69 (41)	71 (48)	103 (100)
1949	72 (35)	70 (50)	87 (85)
1950	63 (27)	72 (54)	91 (87)

through 1953, Y = .576 + .0017(X), was increased slightly by adjusting the intercept from .576 to .600, giving a revised simulated reproductive function of Y = .600 + .0017(X). Simulated population levels generated with the increased reproductive function aligned well with actual population levels through the late 1940's (Fig. 24) but the simulated population still dropped below actual population levels during the 1950's.

The fact that the simulated population remained lower than reported population levels during the 1950's seemed to indicate that even the adjusted reproductive function was not producing realistic calf crops. But inspection of other population parameters indicated otherwise. First, the number of calves per 100 cows generated by the adjusted reproductive function aligned closely with actual calving rates (Table 20). Second, the total number of calves produced annually with the adjusted reproductive function also aligned well with reported calf totals. Those two observations indicated that some simulation parameter other than reproductive rate was incorrect and responsible for the simulated population decline during the 1950's. The most likely remaining source of error was natural mortality estimates.

Although the simulated mortality rate (3 percent) seemed reasonable, it was also the least reliable information used in the simulation. A 3 percent annual herd loss was assumed primarily
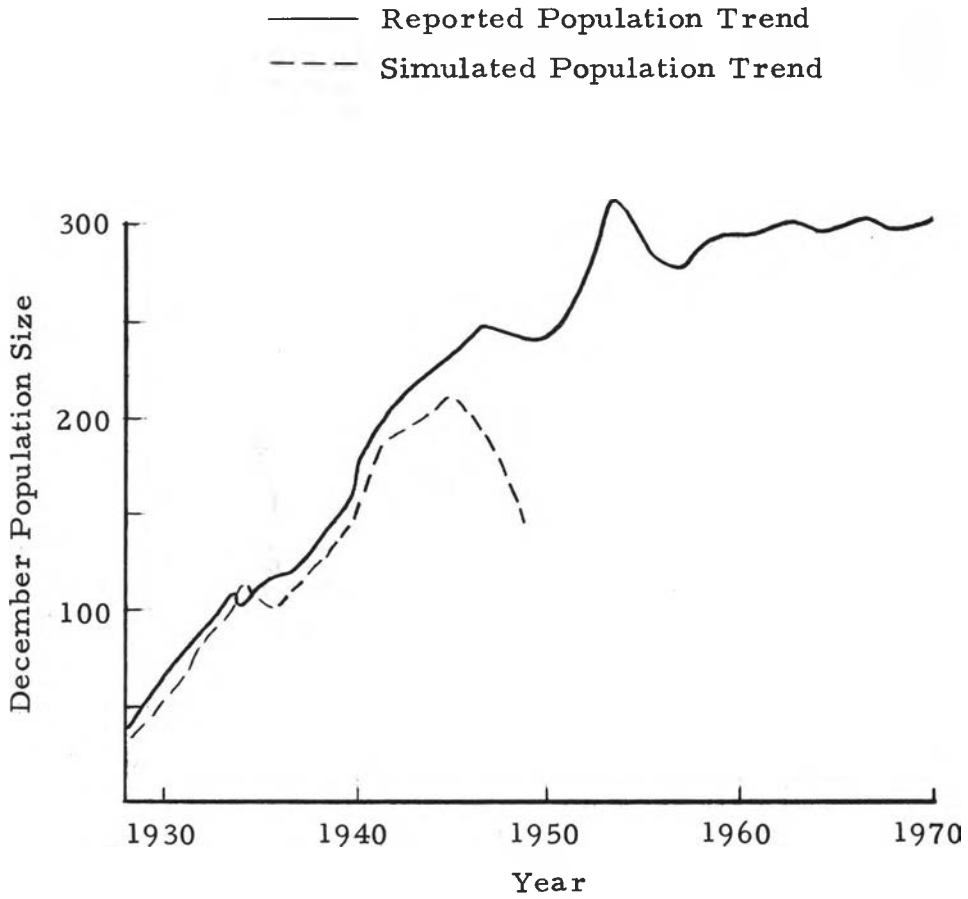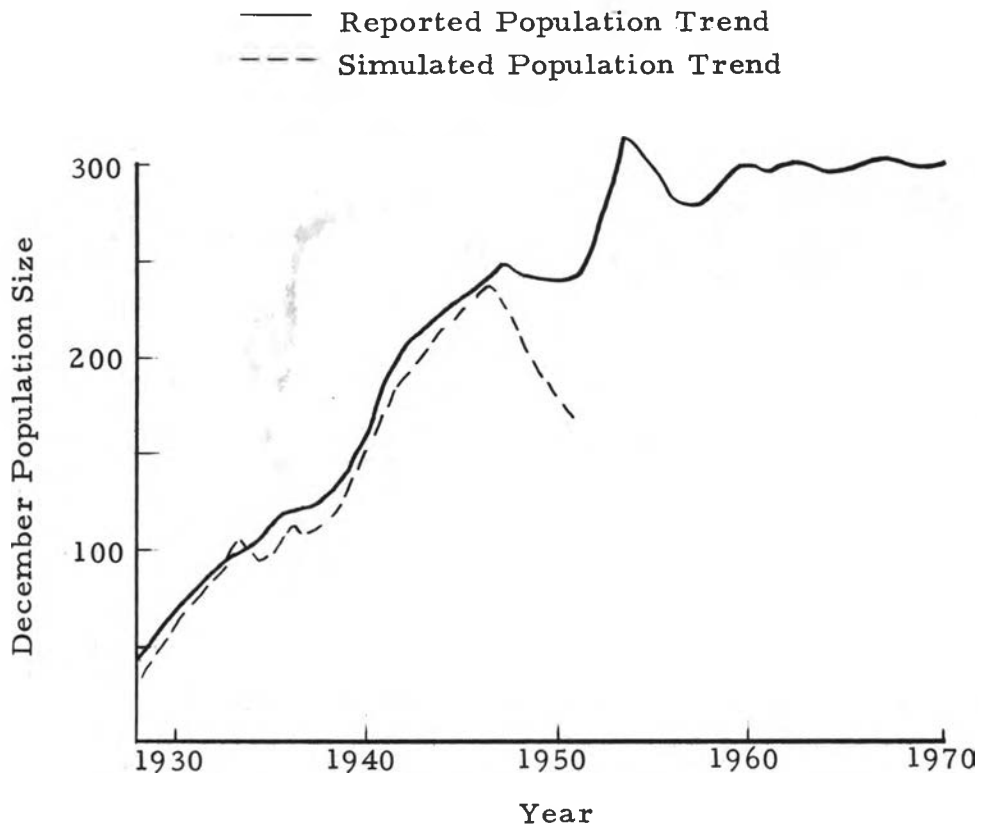
Figure 24. Comparison of reported and simulated herd trend for longhorn cattle on the Wichita Mountains Wildlife Refuge using an adjusted reproductive function after 1945.

Table 20. Alignment of reported and simulated reproductive parameters for longhorn cattle on the Wichita Mountains Wildlife Refuge using adjusted reproductive function after 1945. (Simulated values are in parentheses.)

Year	Calf Crop	Calves Per 100 Cows	Cows Postharvest
1939	27 (32)	52 (55)	65 (62)
1940	33 (36)	51 (54)	80 (78)
1941	41 (40)	51 (52)	91 (88)
1942	52 (48)	57 (50)	99 (97)
1943	44 (40)	44 (48)	93 (91)
1944	51 (53)	54 (53)	108 (106)
1945	58 (54)	54 (51)	113 (110)
1946	61 (59)	54 (52)	111 (110)
1947	63 (60)	57 (59)	97 (95)
1948	69 (62)	71 (64)	103 (100)
1949	72 (68)	70 (69)	87 (85)
1950	63 (60)	72 (68)	91 (87)

because the long-term average mortality level for longhorn cattle
was calculated to be 2 to 3 percent annually. The precise annual
mortality rate was not known. But, if the simulation was correct
with respect to all essential features other than annual mortality
rate, then it would be possible to align simulated and reported popu-
lation sizes and trend during the 1950's by adjusting simulated
mortality level. Through trial and error, the alignment between
reported and simulated population sizes shown in Fig. 25 was ob-
tained by reducing the simulated natural mortality rate from 3 percent
annually to 2.4 percent. The alignment was judged to be good enough
to conclude that the simulation was an acceptable mimic of herd
history through 1954. Consequently, attention was shifted to the last
period of longhorn history to be simulated.

Longhorn Cattle Simulation Results
1955 Through 1972

Longhorn calving rates reported from about 1955 until 1972
were relatively constant. Year to year fluctuations occurred but the
overall variability in calving rates was less than that noted during
earlier periods. The relatively constant calving rates were perhaps
due in large part to the fact that longhorn population size between
1955 and 1972 was also relatively constant, averaging about 300
animals postharvest.
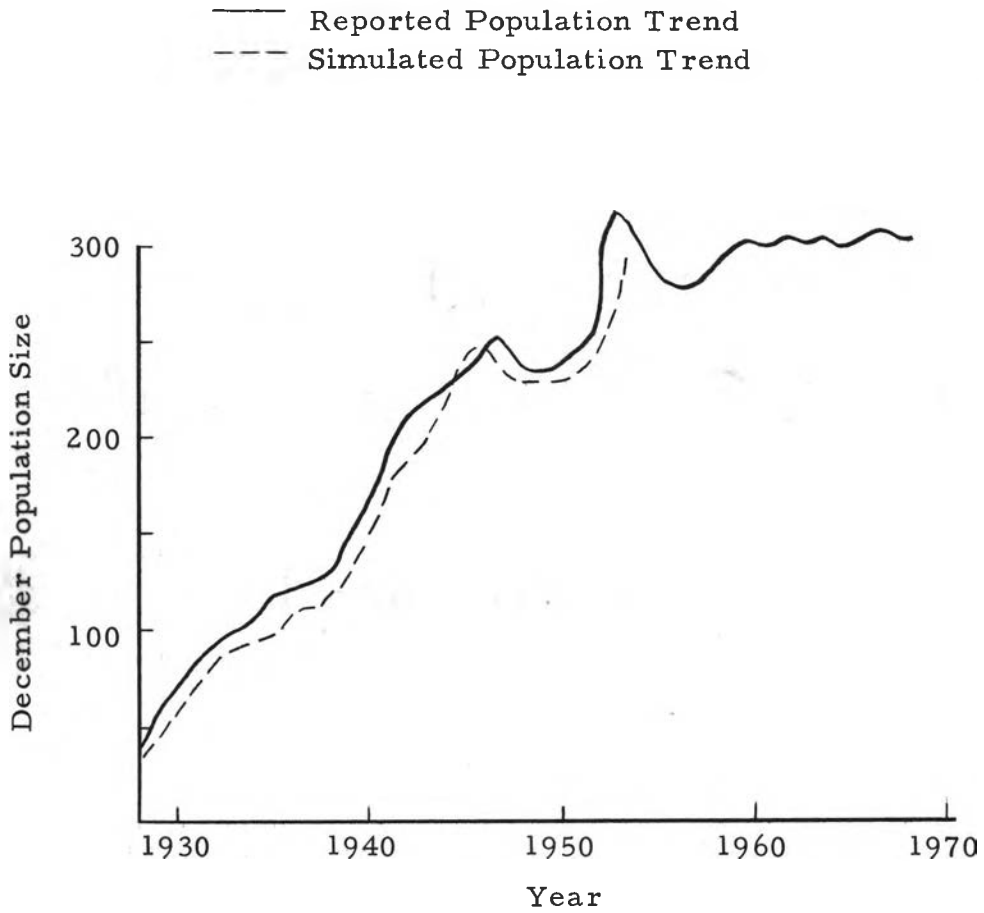
Figure 25. Comparison of reported and simulated herd trend for
longhorn cattle on the Wichita Mountains Wildlife Refuge
(1928-1954) using an adjusted reproductive function plus
an annual mortality rate of 2.4 percent.

Simulations discussed above which dealt with previous years

of longhorn history on the Wichita employed linear regression func-

tions depicting how reproductive rates increased or decreased as

herd size changed over time. Employment of similar regression

functions was not possible in longhorn simulations for years after

1954 because both herd size and reproductive rates were essentially

constant. Thus, to simulate longhorn population dynamics during

those years, an average, constant reproductive rate was used which

yielded the best alignment between reported and simulated population

size and trend when employed in the simulation throughout the entire

period.

The first attempt to simulate longhorn herd history after 1954

employed a constant reproductive rate of 91 percent, i.e., there

were 91 calves produced for each 100 cows 2 years and older in the

herd at time of birth. The simulated reproductive rate closely

approximated the 90.6 percent average birth rate calculated from

field data compiled after 1954. Also, in compliance with reported

information, all reproduction by yearling longhorn females was

removed in the simulation after 1957. Simulated natural mortality

after 1954 was 2.4 percent which matched the mortality level estab-

lished through previous herd simulations, and as was also true of the

simulations for previous years, the total number of longhorns re-

moved annually through simulated harvest equalled reported totals.

That combination of reproductive rates, natural mortality rates and harvest produced a simulated population trend (Fig. 26) which declined rapidly during the 1950's, indicating that at least one (perhaps more) piece of synthesized information used in the simulation was wrong.

Excessive harvest was one possible explanation for the declining simulated population. But it seemed unlikely that simulated harvests were greater than the actual harvests because they equaled reported values and total annual harvest was thought to be accurately known. By the same token, a simulated reproductive rate lower than the actual rate would cause the simulated population to decline if insufficient animals were recruited into the population to offset losses from harvest and natural attrition. But errors in reproductive rate also seemed improbable because the simulated calving rate was virtually identical to the average rate computed from field records and, like total annual harvest, annual calving rates were also among the most accurate pieces of field information available for longhorn cattle. By virtue of being the least reliable information, data compilation errors in mortality rates were concluded as being the most probable explanation for the decline in simulated population size after the mid-1950's.

The simulated mortality level at this point in the analysis was 2.4 percent, the rate derived through simulations for the 1940's.
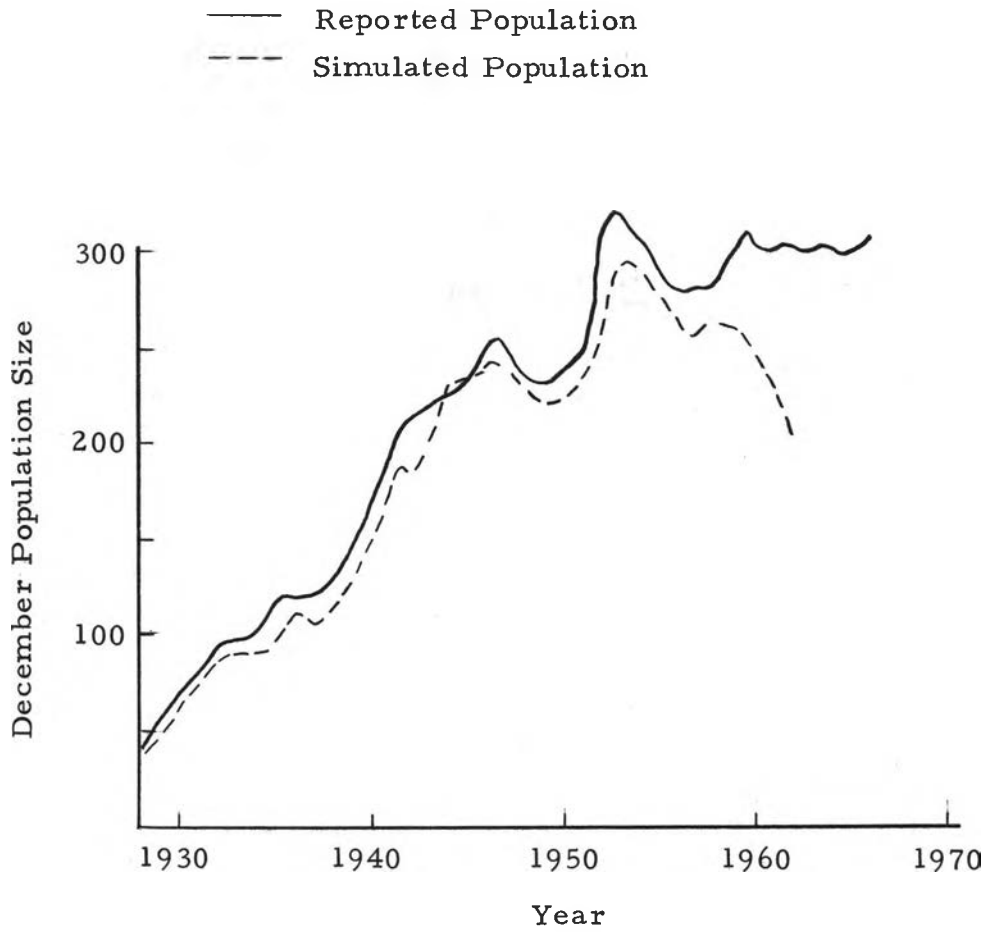
Figure 26. Comparison of reported and simulated population trend for longhorn cattle on the Wichita Mountains Wildlife Refuge assuming a constant reproductive rate of 90.6 percent and a constant mortality rate of 2.4 percent after 1950.

Since the simulated population declined when that rate was used, it appeared that the actual mortality level was less than 2.4 percent annually. However, the period 1955 through 1972 represented a somewhat unique situation in that the simulated population was extremely sensitive to changes in herd mortality level due to the exponential growth established by a constant birth rate (91 calves per 100 cows) and constant death rate (2.4 percent). To illustrate that sensitivity, the simulation described earlier in Fig. 26 declined to "extinction" with a constant birth rate of 91 calves per 100 cows and a constant herd mortality of 2.4 percent. But if mortality level was reduced from 2.4 percent to 1.4 percent (birth rates unchanged), the simulated population "exploded" as illustrated in Fig. 27. Therefore, the simulation of longhorn history between 1955 and 1972 became a matter of "fine-tuning" in that minute adjustment in mortality and reproductive rates were made in an effort to find the combination of birth and death rates which yielded the best alignment attainable between reported and simulated population sizes and trend. The combination finally derived was an average birth rate of 93 calves per 100 cows in combination with a herd mortality of 2.2 percent annually. Population sizes and trend produced by that combination of birth and death rates are compared with actual values in Fig. 28.

To roughly illustrate how precisely Program ONEPOP simulated the entire history of longhorn cattle on the Wichita refuge,
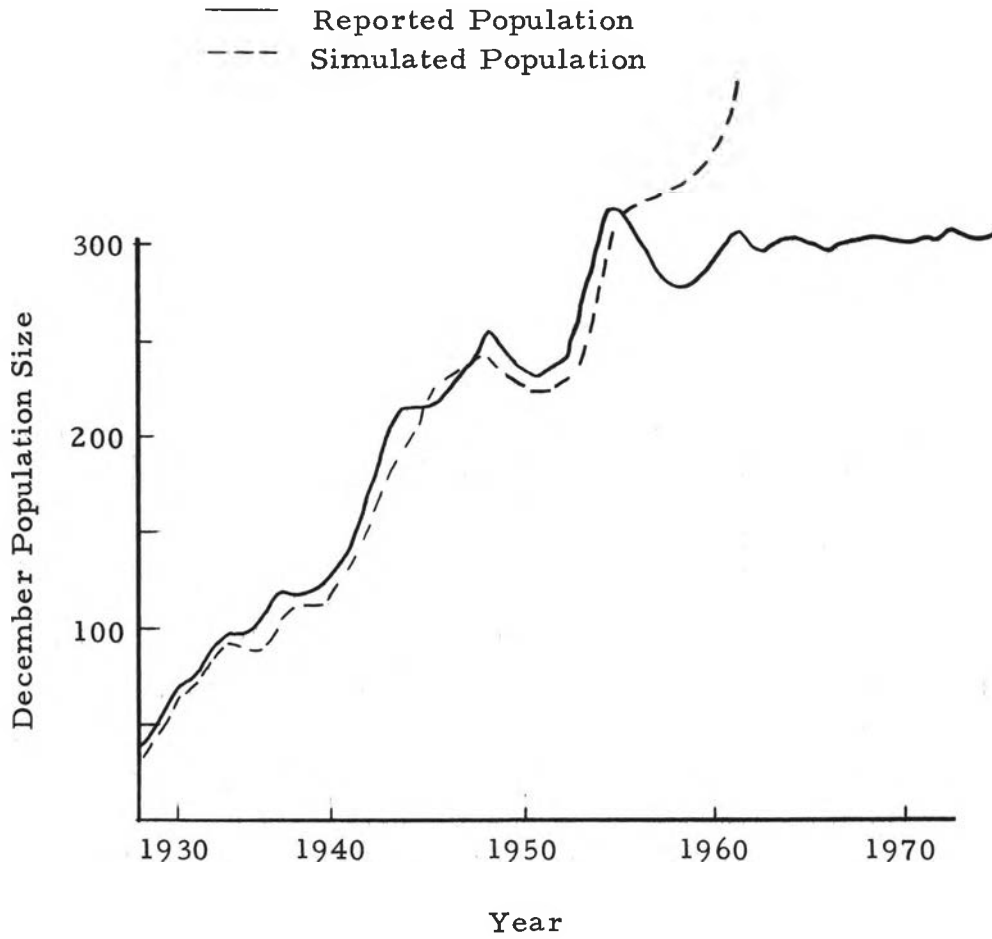
Figure 27. Comparison of reported and simulated longhorn population trend on the Wichita Mountains Wildlife Refuge assuming a constant reproductive rate of 90.6 percent and a constant herd mortality of 1.4 percent after 1950.
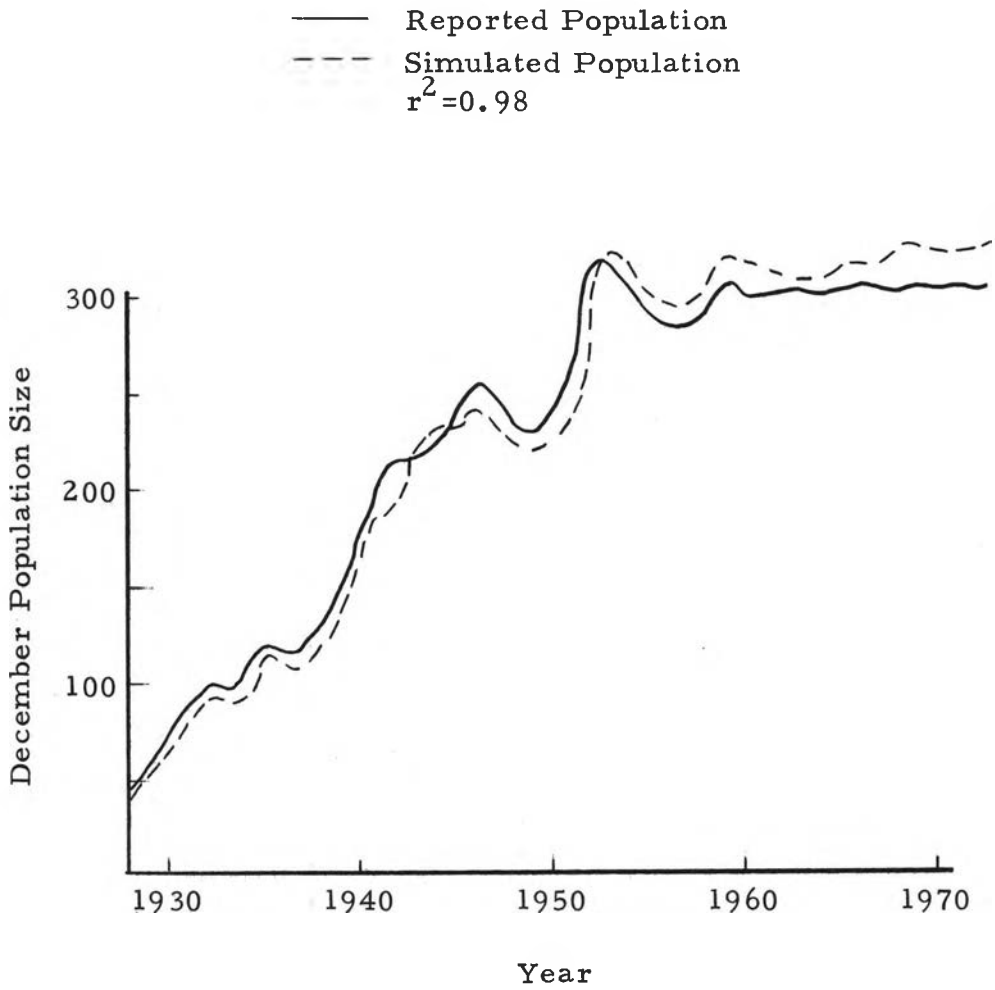
Figure 28. Comparison between reported and simulated population trend for longhorn cattle on the Wichita Mountains Wildlife Refuge. Simulated values reflect the alignment of the final herd simulation.

correlation tests were made between reported and simulated values
for several population parameters. The computed coefficients of
determination (r^2 values) measure the amount of variability in
reported values explained by the simulation. Correlation tests were
made for population parameters associated with herd size and trend
(Fig. 28), reproduction (Table 21) and harvest (Table 22).

The greatest degree of alignment between reported and simu-
lated information, as measured by correlation tests, was with
respect to population size and trend. Simulated herd size did not
exactly align with reported herd sizes between 1955 and 1972 because
simulated values were often 20 to 40 animals greater than corre-
sponding reported values. That population-size discrepancy is
believed due in large part to the assumed constant reproductive and
mortality rates used during the simulation. Perhaps if birth and
death rates had been allowed to vary between years in the simulation,
as no doubt occurred in the real population, better alignment might
have been achieved.

Alignment between reported and simulated reproductive vari-
ables was slightly less than that for population size and trend, with
the poorest reproductive alignment occurring between reported and
simulated calving rates. Frequently, simulated calving rates were
slightly greater than the reported calving rates. The reason for the
higher simulated calving rates is unclear but may be associated with

Table 21. Alignment of reported and simulated reproductive
parameters for longhorn cattle, Wichita Mountains
Wildlife Refuge (final simulation). (Simulated values are
in parentheses.)

Year	Calf Crop	Calves Per 100 Cows	Cows Postharvest
1928	14 (11)	74 --	25 (24)
1929	16 (14)	64 (62)	32 (28)
1930	21 (19)	65 (61)	40 (38)
1931	26 (24)	65 (60)	44 (40)
1932	22 (21)	50 (59)	53 (49)
1933	28 (27)	53 (59)	47 (50)
1934	36 (26)	77 (57)	40 (41)
1935	20 (21)	50 (57)	46 (44)
1936	19 (17)	41 (58)	44 (44)
1937	22 (25)	50 (57)	42 (44)
1938	22 (20)	52 (55)	52 (49)
1939	27 (32)	52 (55)	65 (62)
1940	33 (36)	51 (54)	80 (78)
1941	41 (40)	51 (52)	91 (88)
1942	52 (48)	57 (50)	99 (97)
1943	44 (40)	44 (48)	93 (91)
1944	51 (53)	54 (53)	108 (106)
1945	58 (54)	54 (51)	113 (110)
1946	61 (59)	54 (52)	111 (110)
1947	63 (60)	57 (59)	97 (95)
1948	69 (62)	71 (64)	103 (100)
1949	72 (68)	70 (69)	87 (85)
1950	63 (60)	72 (68)	91 (87)
1951	69 (66)	76 (74)	98 (95)
1952	82 (70)	84 (75)	108 (115)
1953	91 (101)	84 (88)	95 (127)

Table 21. Continued.

Year	Calf Crop	Calves Per 100 Cows	Cows Postharvest
1954	82 (88)	86 (90)	107 (122)
1955	104 (115)	97 (90)	115 (122)
1956	103 (115)	89 (90)	114 (122)
1957	92 (110)	81 (94)	99 (103)
1958	94 (89)	95 (94)	114 (105)
1959	107 (93)	94 (91)	100 (108)
1960	88 (116)	88 (91)	105 (109)
1961	95 (98)	90 (91)	111 (114)
1962	105 (99)	95 (93)	112 (116)
1963	104 (106)	93 (93)	126 (118)
1964	97 (108)	77 (77)	112 (117)
1965	102 (97)	91 (93)	112 (119)
1966	109 (109)	97 (97)	114 (116)
1967	107 (114)	94 (93)	114 (117)
1968	104 (107)	91 (93)	122 (117)
1969	108 (108)	88 (93)	122 (117)
1970	110 (109)	90 (93)	126 (117)
1971	112 (109)	89 (93)	110 (113)
1972	101 (109)	92 (95)	113 (112)
r^2	.984	.848	.922

Table 22. Alignment of reported and simulated removals of longhorn cattle on the Wichita Mountains Wildlife Refuge (final simulation). (Simulated values are in parentheses.)

Year	Calves Harvested	Bulls[1] Harvested	Cows[1] Harvested
1964	40 (47)	18 (22)	17 (26)
1965	43 (48)	20 (19)	20 (25)
1966	53 (55)	24 (22)	26 (28)
1967	53 (52)	22 (24)	23 (22)
1968	43 (45)	19 (18)	20 (24)
1969	59 (53)	20 (28)	19 (25)
r^2	.865	.192	.188

[1]Includes all animals 2 years and older.

alignment between actual and simulated natural mortality. If the
simulated mortality rate slightly exceeds the actual mortality rate,
simulated calving rates would also have to slightly exceed actual
calving rates to compensate and produce the correct population size.
Regrettably, natural mortality was one piece of required information
for which there was little field data available and therefore, even
though considerable effort was made to ascertain the most nearly
correct mortality rate, the simulated mortality level may be slightly
greater than the actual mortality level.

Bison Simulations

Taken as a whole, the reported information base for bison is
good but there are deficiencies, especially with respect to certain
harvest and natural mortality parameters. Deficiencies are similar
to those in reported information for longhorn cattle. For example,
total annual removals of both longhorn cattle and bison have been
recorded on a regular basis; but there is little recorded information
available for either species with respect to the sex and age structure
of the annual removals, at least prior to the 1960's. A second
similarity is that although some information is available on the
general magnitude of bison and longhorn losses from natural causes,
a paucity of information occurred with respect to how those losses
were distributed over age classes and between sexes. Because of the

similarities in their respective data bases, values for missing (or incorrect) bison harvest and natural mortality parameters were approximated in essentially the same manner as described above for longhorn cattle.

Following the compilation and synthesis of population information, the next step in validating Program ONEPOP with respect to the Wichita bison herd was to input the synthesized information and compare simulated output against real-world values. Because of the erratic nature of bison calving rates over time, it was necessary to simulate bison herd history in a step-wise fashion as follows. Attention was first directed to a period of history during which bison demographic conditions were reasonably consistent. Once the simulation was aligned for that period, the next time segment characterized by consistent demographic conditions was simulated.

Bison Simulation Results
1908 Through 1950

Bison reproduction on the Wichita has had a tendency in the past to fluctuate between years. Typically, bison calving rates are "high" for 1 or 2 years and then drop sharply for a few years. Not only have calving rates varied between years, but bison calving-rate trend has also varied over time. Changes in calving-rate trend were apparent from linear regression equations calculated from annual calving rates. The linear regression calculated from bison calving

rates measured between 1908 and 1920 was $Y = .503 - .0013(X)$. The negative slope of that regression indicated calving rates declined as population size increased. But the regression calculated from calving data gathered between 1921 and 1930, $Y = .153 + .0009(X)$, had a positive slope which led to the hypothesis that, after 1920, bison calving rates increased rather than decreased as the population grew in size. The initial bison simulation was designed to test that hypothesis and set simulated reproductive equations exactly as synthesized. Other demographic conditions in the initial simulation were also exactly as synthesized and included (1) an average bison mortality level of 6 percent annually and (2) total annual harvests taken directly from reported materials.

Population sizes and trend generated by the initial bison simulation are compared with actual information in Fig. 29. In general, simulated population sizes and trend aligned well with corresponding reported information until about 1930. Thereafter, the simulated population grew at a rate much faster than the actual population. Inspection of simulated population parameters other than population size and trend revealed the unrealistic simulated population growth probably resulted from incorrectly-synthesized reproductive information.

Comparisons shown in Table 23 indicated that simulated bison calving rates were consistently higher than reported after 1930.

Figure 29. Comparison of reported and simulated population trend (initial simulation) for bison on the Wichita Mountains Wildlife Refuge.

Table 23. Alignment of reproductive parameters obtained in the
first simulation for bison on the Wichita Mountains
Wildlife Refuge. (Simulated values are in parentheses.)

Year	Calf Crop	Calves Per 100 Cows
1908	3 (3)	38 --
1909	3 (4)	27 (48)
1910	5 (6)	50 (47)
1911	7 (6)	58 (47)
1912	9 (8)	50 (46)
1913	10 (9)	63 (45)
1914	5 (10)	24 (44)
1915	10 (12)	45 (42)
1916	21 (13)	70 (41)
1917	16 (15)	40 (39)
1918	12 (17)	26 (37)
1919	21 (19)	38 (35)
1920	28 (21)	44 (33)
1921	17 (20)	24 (29)
1922	19 (23)	23 (30)
1923	30 (26)	34 (31)
1924	27 (27)	30 (31)
1925	28 (30)	28 (32)
1926	42 (32)	39 (34)
1927	35 (35)	30 (34)
1928	52 (41)	38 (35)
1929	60 (44)	41 (36)
1930	57 (48)	33 (37)
1931	46 (56)	23 (39)
1932	54 (70)	28 (43)
1933	62 (85)	34 (47)

Table 23. Continued.

Year	Calf Crop	Calves Per 100 Cows
1934	71 (111)	35 (52)
1935	45 (148)	20 (61)

Whereas the average number of calves per 100 cows between 1930 and 1935 was reported to be 28.8, the average simulated value for the same six-year period was 46.5 calves per 100 cows. Calving information was considered to be among the most reliable field data available for bison. Thus, the discovery that simulated calving rates were substantially higher than reported led to the conclusion that the lack of alignment for population size and trend resulted from an incorrectly synthesized reproductive function. The simulated population produced more calves each year (after 1930) than the actual population had produced, thereby causing it to grow too fast.

The higher simulated calving rates after 1930 were a consequence of increasing calving rates as population increased as per the synthesized regression $Y = .153 + .0009(X)$. Thus, it seemed desirable to calculate a new reproductive equation to more correctly describe bison calving-rate trend after 1930. But it was impossible to calculate such an equation, owing to the variability between years in actual bison calving rates.

Biological mechanisms responsible for the annual variability in bison calving rates during the 1930's (or any other time) are unknown but annual precipitation variations may have been partially responsible. Average annual moisture on the refuge between 1936 and 1940 was 63.8 cm (25.1 in) compared to a long-term (1906-1955) average of 77.2 cm (30.4 in). It is conceivable that, because of low

moisture amounts, total annual forage production on the refuge varied to the extent that bison calving rates were also affected. Regardless of the biological mechanisms involved, the annual variability in calving rates made it impossible to simulate bison herd history after 1930 with linear regression functions which described reproductive trend. Scatter about the calculated regression caused the regression to be an imprecise mimic of reproductive trend. Simulated calf crops were consistently above or below the real calf crop to the extent that close alignment between reported and simulated population sizes was not possible. Consequently, bison history after 1930 was simulated by specifying the exact number of calves born in the population on a year-by-year basis.

The simulation in which annual calf crops were specified also produced population sizes slightly higher than reported population totals (Fig. 30) but population trend was comparable between the two populations. Though the simulated and reported populations were beginning to align, the fact that simulated population sizes were still slightly higher than corresponding reported values indicated that some synthesized information used in the simulation was still wrong. The source of that error was subsequently found to be in simulated natural mortality.

The annual narrative reports mention some heavier-than-normal bison losses on the Wichita during the early 1930's. There
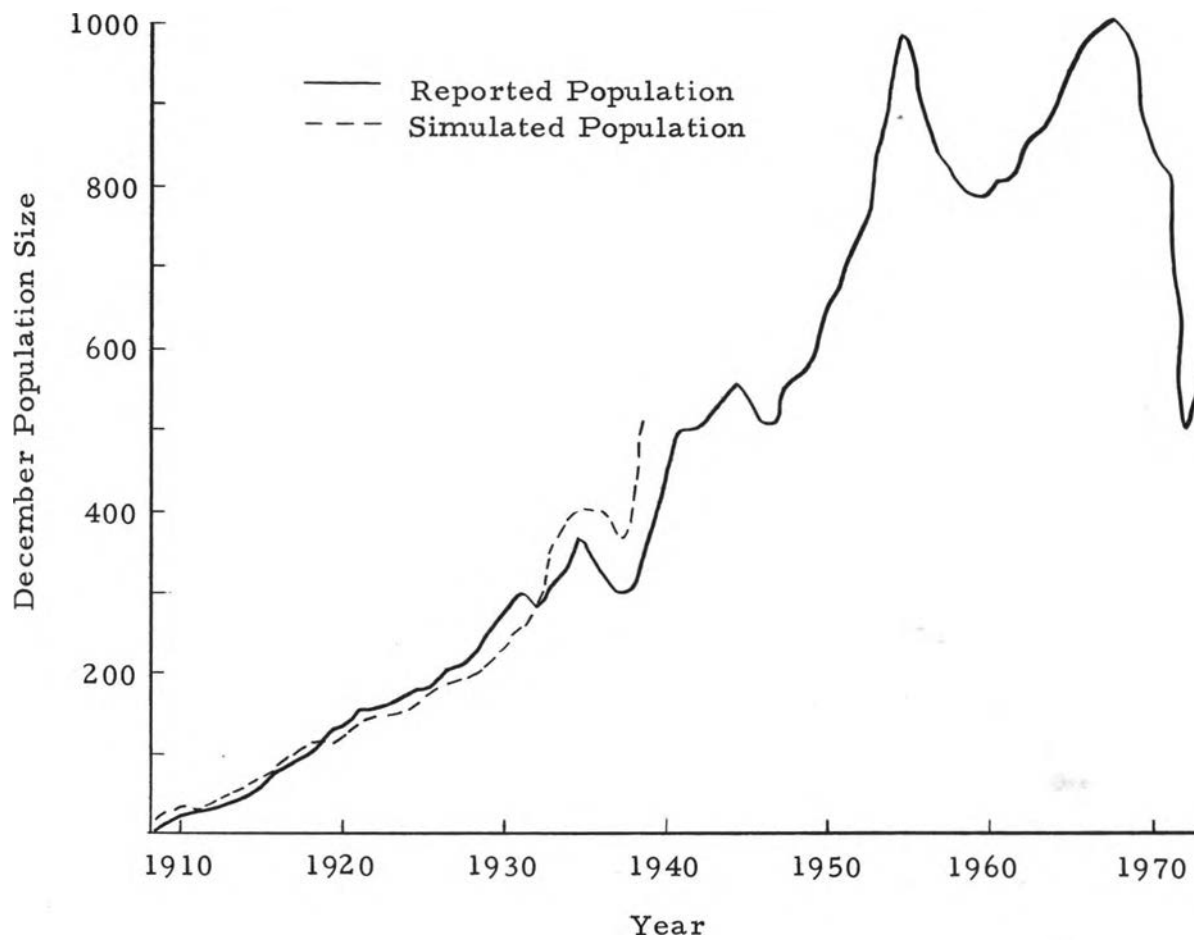
Figure 30. Comparison of reported and simulated population sizes and trend for bison on the Wichita Mountains Wildlife Refuge with simulated calf crops specified after 1930.

were, according to Halloran (1964), between 250 and 300 bison on the Wichita during the early 1930's. If we use the long-term average mortality level of approximately 6 percent (which the simulation did), total bison losses from natural causes would have been 15 to 18 animals per year. Those theoretical losses are in contrast to the 29 bison actually lost in 1931 and the 30 lost in 1932. Those two years represented periods of above-average bison mortality and were not duplicated in the simulation which assumed an <u>average</u> mortality level based upon bison losses throughout the herd's entire history.

Subsequent simulations in which natural mortality rates for the early 1930's were adjusted generated population sizes and trend which closely approximated reported values, as shown in Fig. 31. Alignment between reported and simulated population size and trend was good until about 1950; thereafter the simulated population increased while the actual population decreased in size which indicated that errors in data synthesis were again likely. The next subsection describes how those data-synthesis errors were located and the alignment steps used to bring reported and simulated population levels into alignment after 1950.

Bison Simulation Results
1951 Through 1970

The simulation depicted in Fig. 31 mimicked the actual bison population in several respects: (1) simulated harvest was exactly
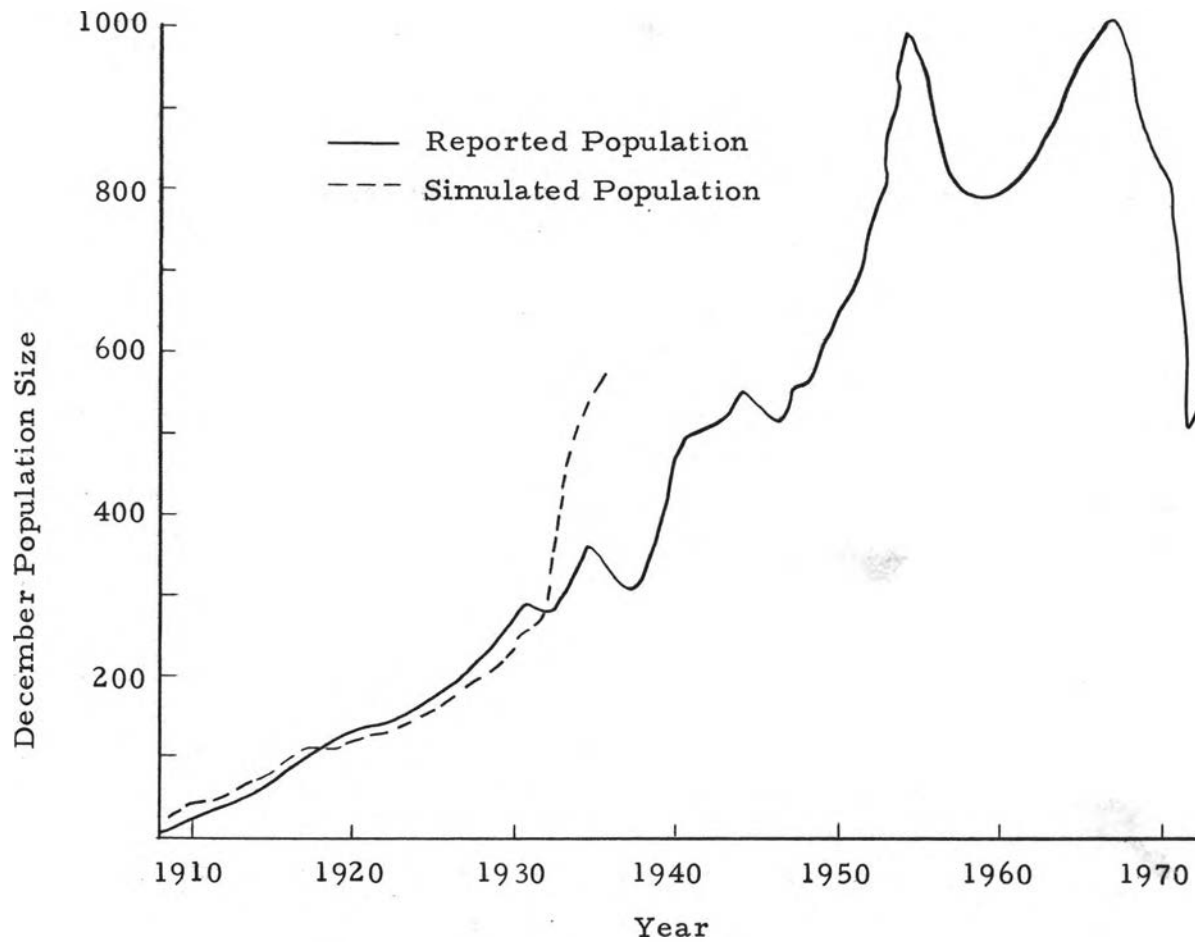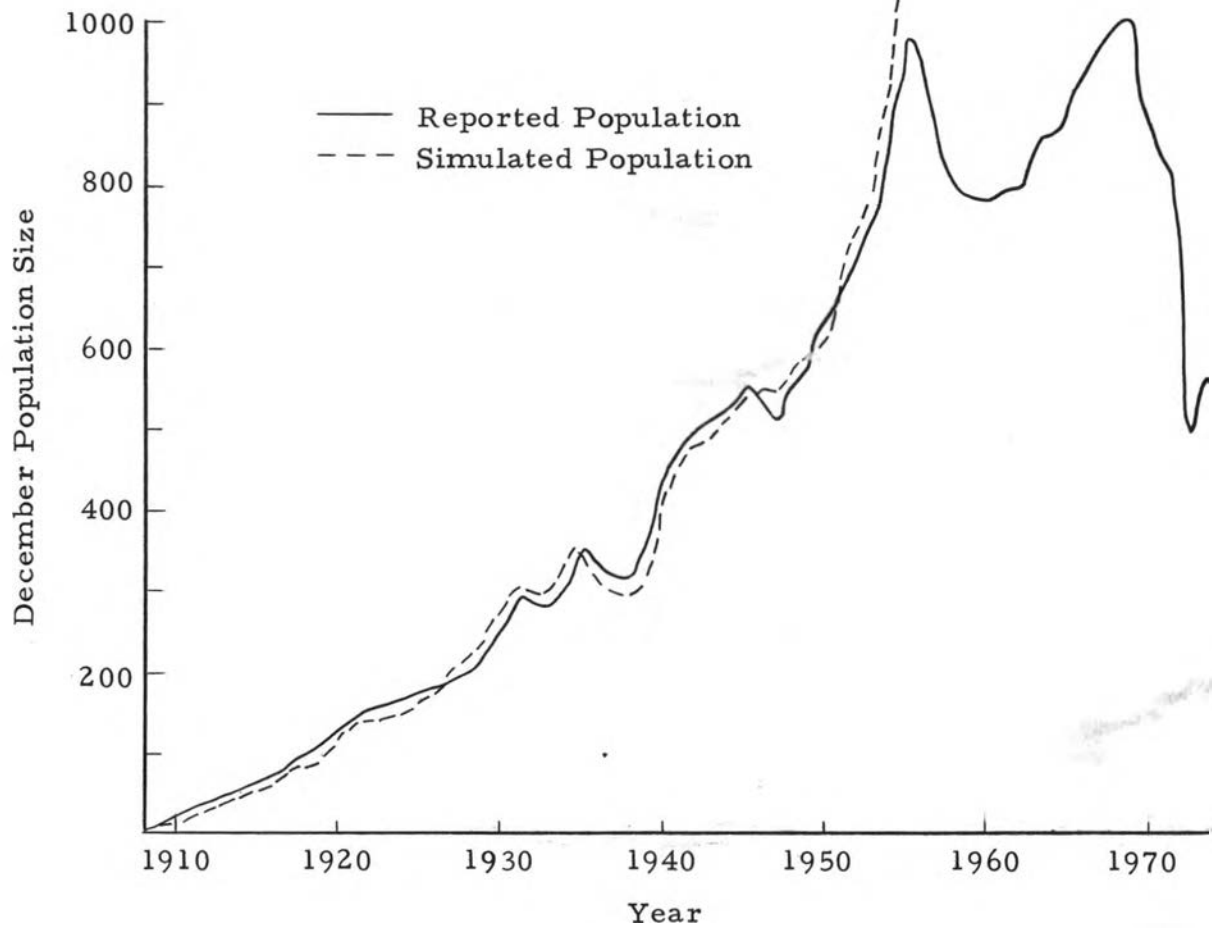
Figure 31. Comparison of reported and simulated population trend for bison on the Wichita Mountains Wildlife Refuge with heavy natural mortality during the 1930's included.

the reported harvest, (2) annual simulated calf crop equalled the reported calf crop, (3) simulated and reported population sizes closely approximated each other through the 1940's and (4) the simulated mortality rate (6 percent) approximated the long-term average bison mortality rate. Though the simulated and real populations were much alike in several respects, the fact that simulated population numbers exceeded reported values during the 1950's led to the inescapable conclusion that some of the demographic information used in the simulation after 1950 was wrong.

Several adjustments in synthesized information could have been made to lower the simulated population and bring it into closer agreement with actual population totals. First, the simulated population could have been lowered by reducing the annual calf crop. As a second alternative, the simulated population could have been lowered by increasing the total number of animals harvested each year. But the reported data for both annual harvest and annual calf crop were thought to be reliable and it made little sense to question the accuracy of the simulation with respect to those two parameters. The least reliable simulated parameter was natural mortality rate and, like harvest and reproductive information, an incorrect natural mortality rate could also account for the higher simulated population after 1950. If the actual mortality level were slightly greater than the simulated mortality rate, that could explain why the real population contained fewer animals than the simulated population.

To determine whether or not the simulated and real populations could be brought into alignment by making only slight adjustments in simulated mortality, the simulated mortality level was incremented in a series of simulations and comparisons made between simulated and reported population levels. The simulated population sizes and trend compared with reported values in Fig. 32 were subsequently obtained by increasing simulated mortality from 6.0 percent to 7.6 percent per year.

Discussions about the bison simulations presented above have centered around only one or two simulation parameters, mainly population size and trend. But the determination of whether or not a simulation is realistically mimicking actual herd dynamics cannot be made on the basis of alignment checks for only one or two parameters. As many parameters as possible should be checked because the likelihood of a realistic simulation increases as additional pieces of the "puzzle" come into alignment with actual data. Accordingly, comparisons for reproductive parameters (total calf crop, calving rate, and breeding-age females) and harvest parameters are presented in Tables 24 and 25 respectively to provide a more comprehensive assessment of how precisely the simulations matched the actual bison population. Tests of statistical correlation were performed to determine the precision with which Program ONEPOP simulated calving rates and the number of breeding-age females in
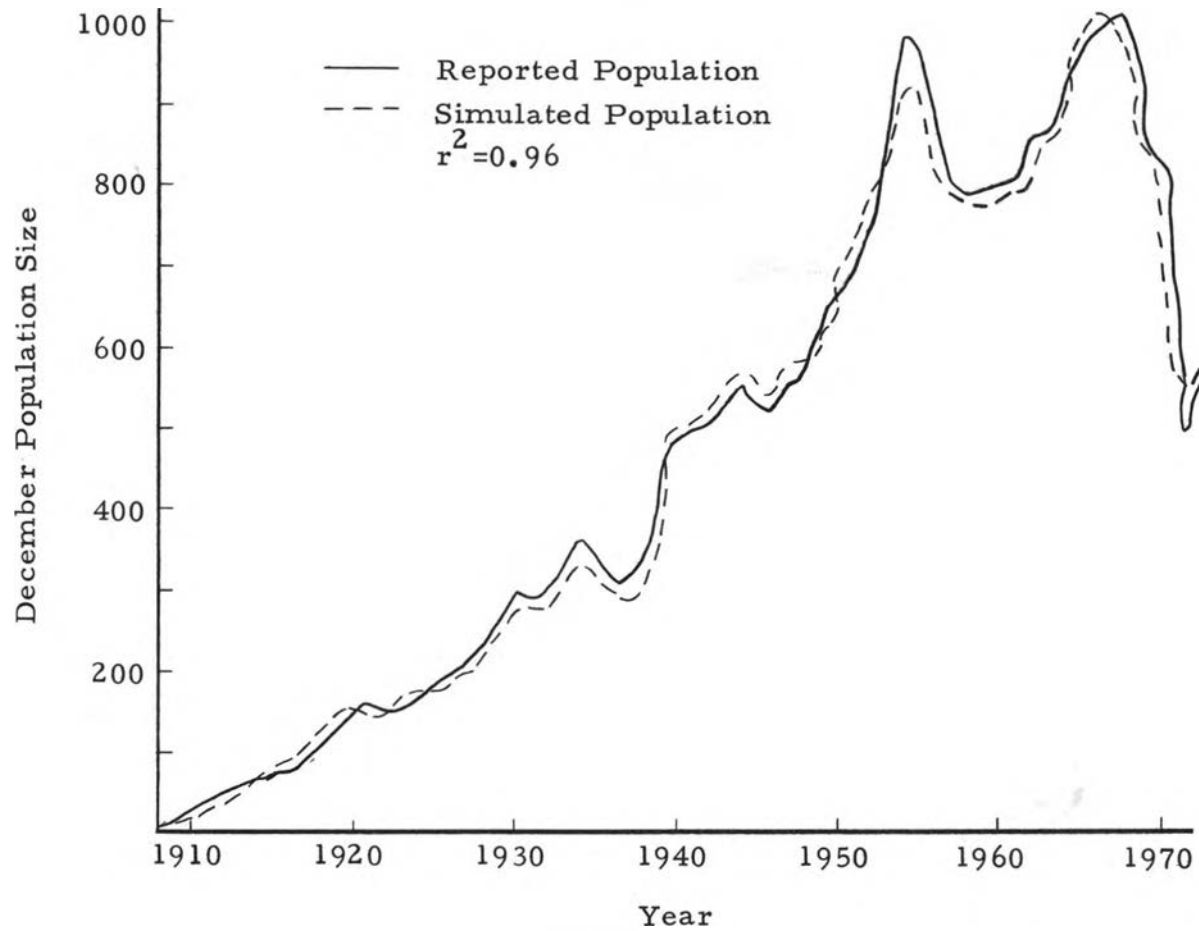
Figure 32. Alignment of population size and trend for bison on the Wichita Mountains Wildlife Refuge with simulated mortality adjusted after 1950.

Table 24. Alignment of reported and simulated reproductive
parameters for bison on the Wichita Mountains Wildlife
Refuge (final simulation). (Simulated values are in
parentheses.)

Year	Calf Crop	Calves Per 100 Cows	Breeding Cows
1908	3 (3)	38 (33)	11 (10)
1909	3 (4)	27 (36)	10 (14)
1910	5 (6)	50 (41)	12 (17)
1911	7 (6)	58 (39)	18 (20)
1912	9 (8)	50 (39)	16 (23)
1913	10 (9)	63 (38)	21 (27)
1914	5 (10)	24 (38)	22 (32)
1915	10 (12)	45 (37)	30 (37)
1916	21 (13)	70 (36)	40 (43)
1917	16 (15)	40 (35)	46 (50)
1918	12 (17)	26 (34)	55 (58)
1919	21 (19)	38 (32)	63 (66)
1920	28 (20)	44 (31)	72 (75)
1921	17 (19)	24 (25)	81 (84)
1922	19 (22)	23 (24)	88 (92)
1923	30 (24)	34 (27)	89 (94)
1924	27 (25)	30 (28)	101 (102)
1925	28 (28)	28 (28)	107 (114)
1926	42 (34)	39 (30)	116 (124)
1927	35 (37)	30 (30)	136 (130)
1928	52 (52)	34 (41)	146 (131)
1929	60 (59)	41 (40)	173 (176)
1930	57 (57)	33 (33)	199 (198)
1931	46 (46)	23 (24)	192 (195)
1932	54 (54)	28 (28)	185 (191)
1933	62 (62)	34 (33)	204 (214)

Table 24. Continued.

Year	Calf Crop	Calves Per 100 Cows	Breeding Cows
1934	71 (71)	35 (34)	226 (240)
1935	45 (45)	20 (19)	196 (197)
1936	82 (82)	42 (42)	194 (197)
1937	53 (53)	27 (27)	197 (186)
1938	74 (74)	38 (40)	218 (218)
1939	112 (112)	51 (52)	249 (252)
1940	114 (114)	46 (46)	290 (294)
1941	78 (78)	27 (27)	302 (286)
1942	106 (106)	35 (37)	317 (324)
1943	129 (129)	41 (41)	330 (346)
1944	121 (121)	37 (35)	313 (324)
1945	107 (107)	34 (33)	282 (289)
1946	121 (121)	43 (42)	259 (263)
1947	140 (140)	54 (54)	302 (306)
1948	77 (77)	25 (25)	346 (331)
1949	156 (156)	45 (47)	388 (387)
1950	190 (190)	49 (50)	402 (403)
1951	155 (155)	39 (39)	420 (421)
1952	190 (190)	45 (39)	420 (451)
1953	183 (183)	41 (41)	488 (487)
1954	271 (271)	55 (56)	530 (528)
1955	213 (213)	40 (41)	514 (510)
1956	270 (270)	53 (54)	489 (484)
1957	234 (234)	48 (49)	459 (456)
1958	168 (168)	37 (37)	455 (455)
1959	199 (199)	44 (44)	458 (461)
1960	195 (195)	60 (54)	471 (470)
1961	137 (137)	48 (37)	459 (440)

Table 24.   Continued.

Year	Calf Crop	Calves Per 100 Cows	Breeding Cows
1962	193 (193)	52 (52)	487 (484)
1963	184 (184)	55 (48)	388 (412)
1964	206 (206)	53 (51)	436 (450)
1965	205 (205)	47 (56)	443 (416)
1966	226 (226)	51 (55)	372 (397)
1967	254 (254)	68 (65)	332 (372)
1968	230 (230)	69 (63)	303 (358)
1969	135 (135)	44 (38)	294 (351)
1970	160 (160)	54 (46)	275 (354)
r^2		.920	.980

Table 25. Comparison of reported and simulated harvests for bison on the Wichita Mountains Wildlife Refuge (final simulation). (Simulated values are in parentheses.)

Year	Males Harvested	Females Harvested
1962	59 (59)	41 (41)
1963	68 (68)	62 (62)
1964	79 (79)	40 (40)
1965	69 (69)	35 (35)
1966	73 (73)	128 (128)
1967	91 (91)	139 (139)
1968	122 (122)	141 (141)
1969	115 (115)	116 (116)

the herd. Correlation tests were not carried out on total annual calf
crop and annual harvest because both of those parameters were set
in the simulation (though calf crops were not set prior to 1930) to
equal actual values and therefore statistical tests were largely in-
appropriate.

Elk Simulations

Elk habitat on the Wichita differs from that used by either
bison or longhorn cattle. In contrast to the open grasslands and
parks preferred by longhorn cattle and bison, elk tend to concentrate
in remote sectors of the refuge characterized by dense stands of
blackjack oak and steep-to-moderate terrain (Halloran 1958). The
rugged nature of elk habitat makes it difficult to acquire information
on the herd and has forced the refuge biologist to rely upon data-
gathering procedures which typically lack the directness of the tech-
niques used to obtain information about longhorn cattle and bison.
For example, whereas bison and longhorn cattle can be manuvered
into corrals and systematically counted, elk are censused from
helicopter flights over concentration areas. A second difficulty
involves the collection of reproductive information. Bison and
longhorn calves can be counted directly but elk reproduction must be
approximated from fetus counts or by locating breeding harems and
estimating calf:cow ratios.

Difficulties connected with data acquisition has regrettably led to the reporting of some dubious information for elk. Bartnicki's (1969) criticisms of elk census methods used on the refuge during the 1960's exemplify the questionable elk data. Bartnicki observed that in some years elk counts were not made and, that when counts were made, often large "correction factors" were used to arrive at the reported total.

Although field data for elk are deficient in some respects, sufficient information was extracted from the files with which to simulate herd history. Elk history, like that of longhorn cattle and bison, was simulated in a step-wise manner. The length of time during which elk have existed on the refuge was broken down into time segments, each segment representing a period of time during which elk demographic conditions were somewhat uniform and distinct from those of other time segments. Three time segments, established on the basis of variation in elk calving trend, were simulated. Once the simulation was aligned for a given time segment, the simulation was extended to include the next segment. Simulated results for the first time segment, 1913 through 1940, compared with reported data as follows.

Elk Simulation Results
1913 Through 1940

Historical accounts suggest that the Wichita elk population grew in a more-or-less gradual manner after it was established.

According to data compiled by Halloran (1963), field counts conducted by the U.S. Forest Service, which administered the refuge during its early period, determined that the population increased from the original transplant of 20 animals in 1912 to 125 elk by 1922. The population contained an estimated 300 elk in 1925 and 222 by 1935. The accuracy of those early counts has not been established but they should be representative enough to indicate population trend. During the 1920's and 1930's, elk on the Wichita were confined to the Buffalo Pasture, an 8000-acre (3250-ha) fenced range unit lacking much of the rugged terrain typical of present-day elk habitat. Thus, even though the early counts were made on foot or horseback, and undoubtedly some elk were not counted, sufficient numbers of elk should have been counted to determine whether the population was increasing, decreasing or remaining stable.

Elk simulations using demographic input exactly as synthesized from the early field records produced a population trend (Fig. 33) which increased steadily after 1913 and which, also like the reported population, attained a level of approximately 300 elk by the mid-1920's. The strong similarities in growth for both the reported and simulated populations indicated that the simulated population increased over time much like the actual population. But it was impossible to compare reported and simulated values for other population parameters, owing to a lack of reported data. The early reports provided

Figure 33. Comparison of reported and simulated population levels for elk between 1913 and 1940 on the Wichita Mountains Wildlife Refuge.

some estimates of population sizes and harvests but little information
on other population parameters as calf crop size, mortality losses
or herd structure.

The most obvious difference between the simulated and real
populations occurred during the late 1920's. Though sparse, the
elk counts which were available suggested that the real population
may have decreased slightly during the late 1920's or 1930's from
about 300 elk in 1925 to approximately 220 in 1935. The simulated
population did not decline during that period. While a slight decline
in population level was indicated, nothing was found in the records
which indicated what event(s) caused the decline. Elk harvesting
began on the Wichita in 1925 and could possibly have caused a popu-
lation decline. But, if the population declined in response to annual
harvesting, then the simulated population would have also declined
because the number of elk removed through simulated harvest was
nearly identical to the number of elk actually harvested, a conclusion
supported by the data comparisons in Table 26.

There were other possible demographic explanations for the
lower reported population sizes. For example, natural losses might
have been unusually heavy during those years or calving rates might
have declined. But the most likely explanation was poor census. The
refuge supervisors report for 1930 contains the following statement
(Anonymous 1930:6):

Table 26. Comparison of reported and simulated values for elk
harvested on the Wichita Mountains Wildlife Refuge
between 1925 and 1940. (Simulated values are in
parentheses. [1])

Year	Males Harvested	Females Harvested	Total Harvest
1925	2 (2)	9 (9)	11 (11)
1926	2 (2)	11 (11)	13 (13)
1927	-- (8)	-- (9)	17 (17)
1928	-- (0)	-- (0)	-- (0)
1929	1 (1)	24 (23)	25 (24)
1930	-- (0)	-- (0)	-- (0)
1931	-- (0)	-- (0)	-- (0)
1932	23 (23)	12 (12)	35 (13)
1933	-- (25)	-- (25)	50 (50)
1934	-- (1)	-- (1)	2 (2)
1935	-- (0)	-- (0)	-- (0)
1936	4 (4)	9 (8)	13 (12)
1937	23 (23)	16 (16)	39 (39)
1938	10 (10)	18 (18)	28 (28)
1939	15 (15)	15 (15)	30 (30)
1940	5 (5)	8 (8)	13 (13)

[1] For years in which only the total number harvested was
reported (e.g., 1927), a 50:50 sex ratio in the harvest was assumed.

"It must be remembered the number (of elk) shown
as on hand is only on estimate. I am free to admit that
I have never felt very secure about the number reported.
A rather extended effort was made last season to effect
a count by air plane, but without the desired result."

The supervisor's statement implies more elk were on the refuge
than actually counted and reported. Because there was some question
about the accuracy of the reported population totals and therefore
about whether or not the population had even declined, the differences
between reported and simulated population levels did not seem to
justify concluding that the simulation was an unrealistic mimic of elk
population history. Therefore, efforts were undertaken to extend the
simulations to include the next segment of elk history.

Elk Simulation Results
1941 Through 1955

The Wichita refuge was administered by the U.S. Forest
Service until 1936 at which time administrative duties were trans-
ferred to the U.S. Biological Survey. Elk counts made by the
Biological Survey during the 1940's and early 1950's indicated the
refuge population remained fairly stable and averaged about 200
animals (December count).

Simulations which reproduced herd history during the period
also produced a fairly stable population (Fig. 34) but the simulated
population consistently contained about 100 elk more than what field
counts indicated. Although the simulated population did not agree
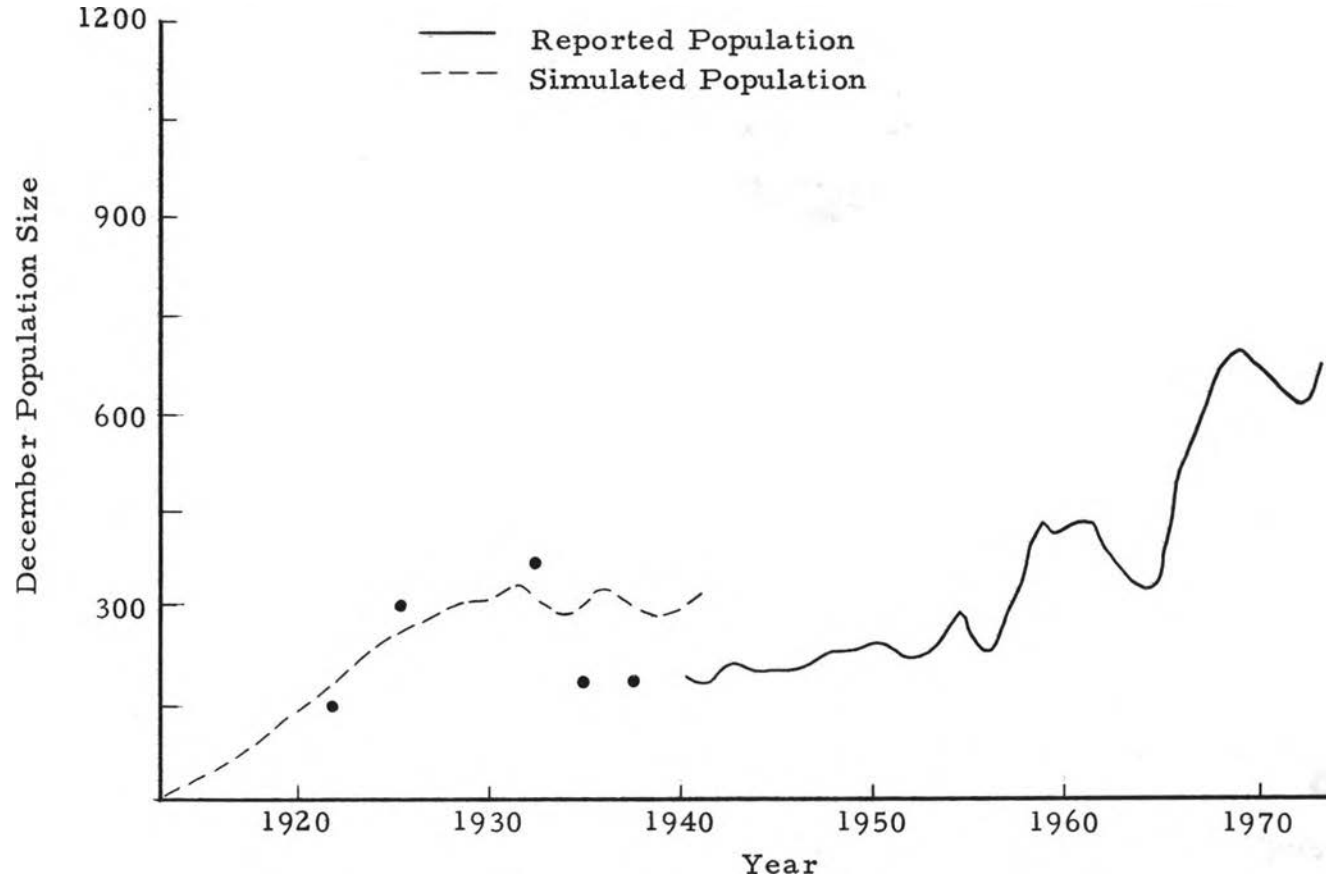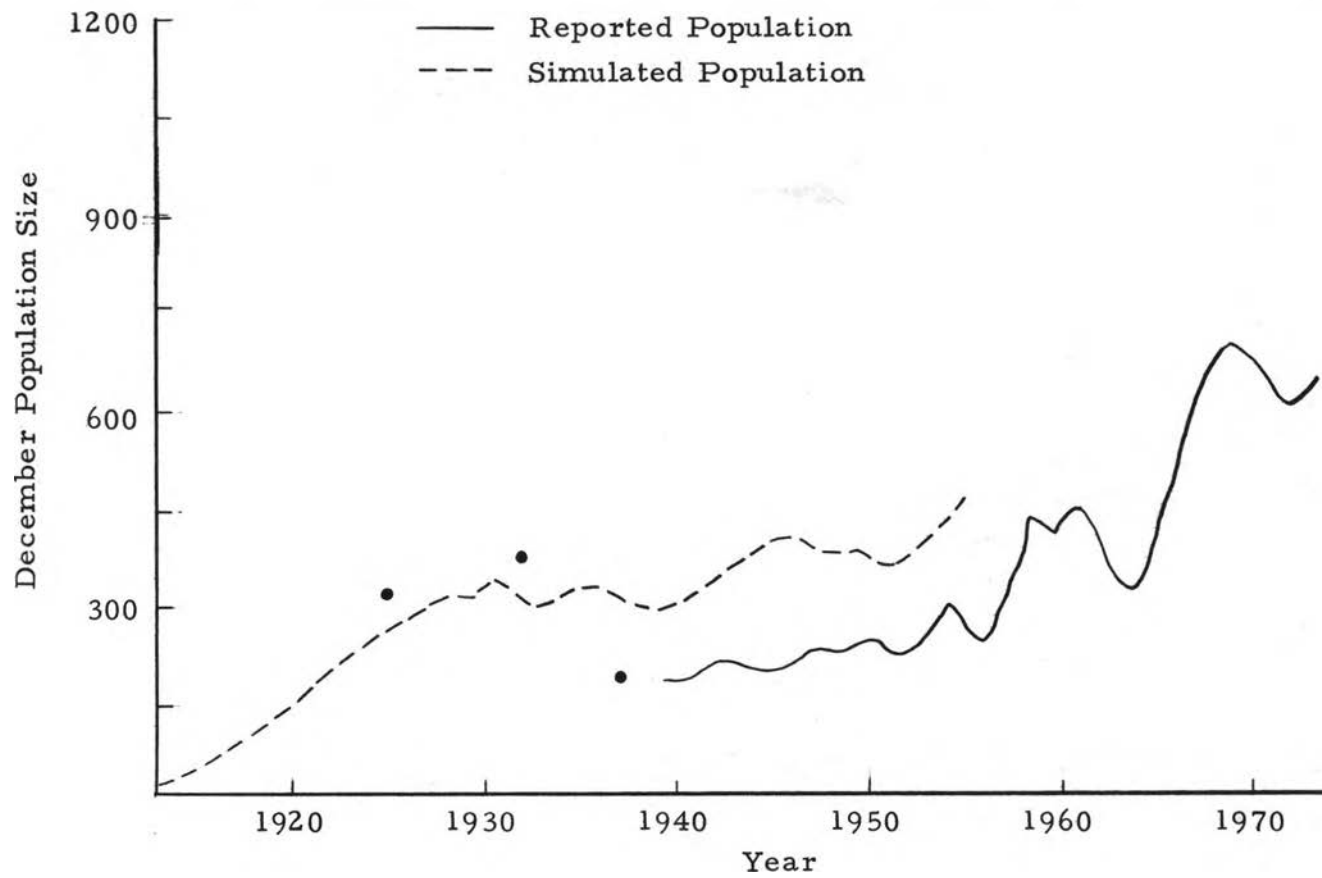
Figure 34. Comparison of reported and simulated population levels for elk between 1913 and 1954 on the Wichita Mountains Wildlife Refuge.

with reported population totals, it did agree with other reported

population information. For example, the calving rates produced by

the simulated calving function, $Y = .378 + .0002(X)$, were roughly

comparable to the calving rates calculated for the herd from reported

calf sighting and incidences of pregnancy (Table 27). The simulated

population also agreed with the real population in the number of elk

harvested each year, also evident from comparisons in Table 27. A

third way in which the simulated population closely matched reported

information was with respect to natural mortality rate. The simu-

lated mortality rate (5 percent annually) agreed with the average loss

rate Halloran (1963) reported for the herd.

The fact that the simulated population contained more elk than

reported for the actual population was confusing, especially since

the simulated and reported populations agreed with respect to several

other population parameters. The population-size discrepancy

seemed to indicate that one or more of the population parameters for

which the populations were aligned was incorrect and that modifica-

tions would have to be made in certain simulated parameters to align

the two populations. But comments entered into the elk records

made incorrectly-synthesized field data a less likely explanation for

the population-size discrepancies than incorrect reported population

estimates. Frequently comments were found in the records that the

reported herd counts were considered to be "conservative estimates,"

Table 27. Comparison of reported and simulated values for elk
reproduction and harvest during the period 1937 through
1955, Wichita Mountains Wildlife Refuge. (Simulated
values are in parentheses.)

Year	Calves Per 100 Cows	Males Harvested	Females Harvested
1937	-- (30)	23 (23)	16 (16)
1938	-- (29)	10 (10)	18 (18)
1939	-- (40)	15 (15)	15 (15)
1940	-- (42)	5 (5)	8 (8)
1941	10 (44)	6 (6)	17 (17)
1942	25 (46)	1 (1)	1 (1)
1943	35 (48)	12 (12)	6 (6)
1944	35 (50)	14 (14)	13 (13)
1945	20 (52)	11 (11)	9 (9)
1946	60 (54)	21 (21)	38 (38)
1947	-- (56)	45 (45)	37 (37)
1948	40 (58)	22 (22)	23 (23)
1949	55 (60)	26 (26)	25 (25)
1950	60 (62)	28 (28)	41 (41)
1951	60 (64)	20 (20)	24 (24)
1952	87 (66)	21 (21)	16 (16)
1953	55 (68)	16 (16)	18 (18)
1954	-- (70)	17 (17)	18 (18)
1955	30 (72)	2 (2)	3 (3)

alluding to the probability of more elk on the refuge than what had

actually been seen during census. Those statements alone justified

the acceptance of the higher simulated population numbers. But

additional justification for accepting the simulated population totals

was found in other reported statements that significant numbers of

elk had actually left the refuge and moved onto rangelands adjoining

the refuge. Halloran (1963) estimated 40 elk inhabited areas outside

the refuge boundaries in 1955. Those off-refuge elk were not included

in the refuge population estimates but are included in the simulated

population totals. The reported population numbers are not so much

inaccurate as they are incomplete. Thus, there was little compelling

evidence that the simulation was not providing a true representation

of elk numbers during the 1940's and early 1950's. With that thought

in mind, the simulation was extended into later years.

Elk Simulation Results
1956 Through 1972

Commencing with the mid-1950's, the refuge employed a dif-

ferent field procedure to acquire information about the number of elk

on the refuge. Helicopter pilots from nearby Fort Sill Military

Reservation began flying refuge staff members over known elk con-

centration areas in efforts to locate and count the entire refuge popu-

lation, although elk outside refuge boundaries were still not counted.

Frequently, the flights were made on two consecutive days and then

later supplemented with ground counts. There can be little question but that the helicopter flights greatly increased the refuge staff's ability to traverse the refuge and to locate elk. But, in spite of that increased coverage, not all elk were located and counted. For example, Halloran (1960a) described how 33 elk known to be in certain areas of the refuge were not seen during flights over those areas. The knowledge that not all elk were being seen and counted led in turn to the adoption of a 15 percent "error-correction" factor; the number of elk actually seen was increased by 15 percent to arrive at the estimated total refuge population.

Population counts obtained through aerial census indicate that the growth pattern of the Wichita elk herd changed rather drastically during the 1950's and 1960's from what it had been during previous years. During the 1930's and 1940's, the herd was described as being rather constant in size from one year to the next, a conclusion supported not only by field counts but also by simulations for those years. However, field surveys carried out during the late 1950's located considerably more elk than what had been counted previously and led the refuge biologist to conclude that the herd was rapidly increasing. It is uncertain to what extent the higher census totals were due to actual population increases and to what extent they reflected the better coverage of elk concentration areas afforded by helicopter flights. In either case, the refuge responded to the higher

population estimates by increasing total annual harvests. Whereas

an average of 37 elk were removed annually on the refuge between

1950 and 1955, the average increased to 60 elk between 1956 and 1960

with a high of 121 elk removed in 1960. Simulations with Program

ONEPOP support the refuge biologists' conclusion that the elk popu-

lation increased during the 1950's and 1960's. But those simulations

also reveal that, if the reported counts are truly indicative of the

number of elk on the refuge itself, then the off-refuge population had

to be substantially larger than originally believed.

Field counts suggest the refuge population increased from about

300 elk in 1955 to an all-time high of about 700 in the late 1960's as

depicted in Fig. 35. Again, it should be stressed that the refuge

counts do not include elk known to be inhabiting rangelands outside

the actual refuge boundaries. The graphic comparison between

reported and simulated population totals in Fig. 35 shows the extent

to which the reported herd counts apparently underestimated the

actual number of elk on the refuge, or at least in the immediate

vicinity of the refuge. Whereas the reported counts indicated a

maximum population of about 700 elk, the simulation showed that the

maximum was closer to 1100 elk, an increase of 57 percent over the

refuge figure.

In view of the sizable difference between the refuge population

estimates and what the simulation produced, it might seem only
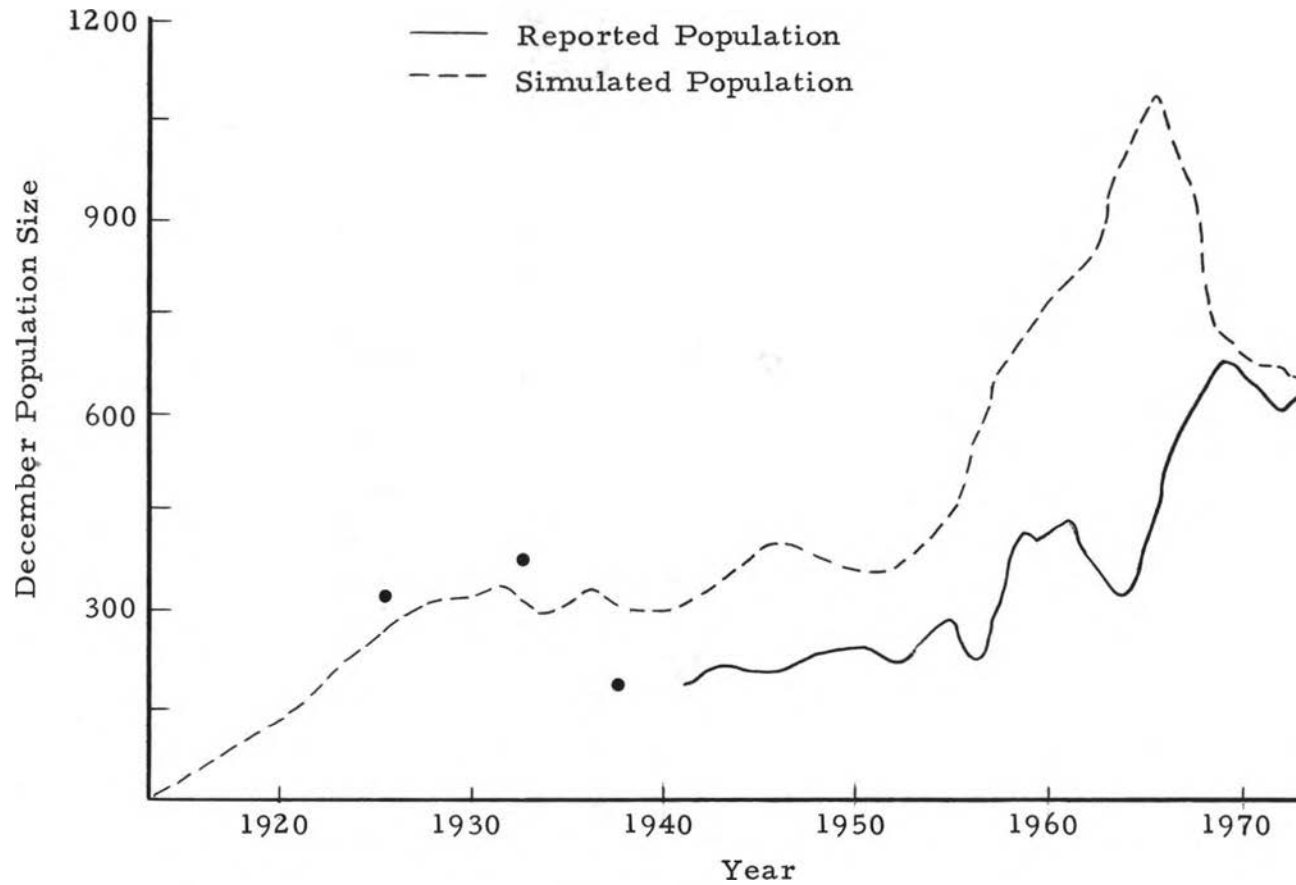
Figure 35.   Comparison of reported and simulated population size and trend for elk on the Wichita Mountains Wildlife Refuge, 1913 through 1972.

prudent to question the accuracy of the simulation. Efforts had been made to base the simulation entirely upon reported field data. But perhaps the simulated elk population exceeded the reported population because of greater recruitment caused by an incorrectly-synthesized calving function. As a second possibility, perhaps the simulated population exceeded the reported population because fewer elk were harvested in the simulation than what had been actually taken from the real population.

To determine whether or not those possible data-synthesis errors had actually been made, the comparisons shown in Table 28 were drawn to cross-check reported and simulated harvests and calf crops. The comparisons show that the simulated harvest was almost exactly the same as the reported harvest. But the comparisons also reveal that the simulated calf crops greatly exceeded the reported calf crops. Clearly the major demographic difference between the two populations (other than population size) was with respect to the amount of recruitment into the population each year.

Acting solely in response to the comparisons in Table 28, one might logically conclude that the simulated population size was un-realistic, citing the larger simulated calf crops as justification for that argument. But before deciding that the simulated calving rate was not correct and that the simulated population was unrealistically large, it seemed equally prudent to conduct one additional test. In

Table 28. Comparison of reported and simulated values for elk
reproduction and harvest on the Wichita Mountains
Wildlife Refuge, 1956-1972. (Simulated values are in
parentheses.[1])

Year	Calves Produced	Males Harvested	Females Harvested
1956	38 (108)	10 (10)	12 (12)
1957	60 (138)	11 (11)	20 (20)
1958	79 (145)	24 (24)	28 (28)
1959	50 (152)	37 (40)	38 (35)
1960	81 (165)	60 (63)	61 (58)
1961	75 (162)	45 (45)	68 (68)
1962	59 (156)	45 (45)	31 (31)
1963	51 (183)	29 (29)	20 (20)
1964	61 (210)	44 (44)	42 (42)
1965	90 (212)	65 (65)	58 (58)
1966	173 (214)	121 (119)	133 (131)
1967	175 (179)	164 (157)	152 (145)
1968	93 (149)	121 (120)	156 (154)
1969	113 (114)	63 (63)	83 (83)
1970	147 (118)	93 (92)	79 (79)
1971	71 (108)	42 (42)	75 (75)
1972	240 (90)	70 (70)	113 (112)

[1] A 50:50 sex ratio in the harvest was assumed for 1959 and
1960.

view of the accelerated elk harvesting program on the refuge during the late 1950's and also the fact that the refuge population had been consistently underestimated for some time, we should determine whether or not it is mathematically possible for an elk population containing the number of elk reported on the refuge to maintain itself (let alone increase as field data indicated) while also sustaining the record annual harvest known to have been attained between 1955 and 1972.

To determine whether or not the Wichita elk population could have contained the reported number of animals and simultaneously supported the reported annual harvests, a separate, hypothetical simulation was carried out based upon the following demographic conditions: (1) the initial population contained the number of elk reported in December 1954 plus the number of calves counted in 1955, (2) all adult females plus 60 percent of all yearling females produced a calf each year, (3) natural mortality was set to zero, and (4) simulated annual harvests coincided exactly with reported figures. The results of that hypothetical simulation are shown in Fig. 36 and clearly indicate that a population containing the reported number of elk could not possibly maintain itself and simultaneously support the annual harvests recorded on the refuge, even under conditions of maximum reproduction and minimum natural losses.
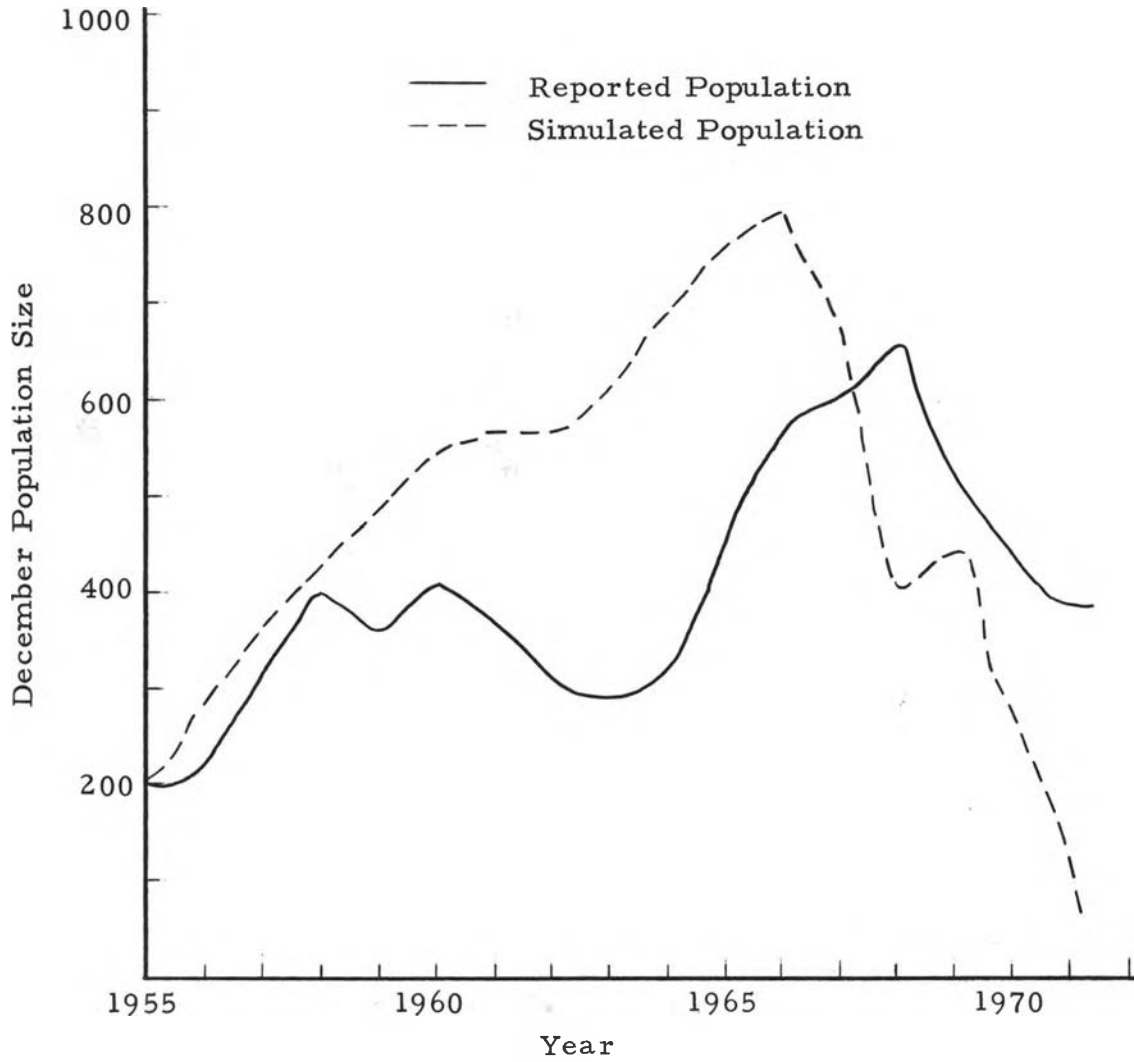
Figure 36. Comparison of hypothetical simulated population trend and reported population trend for elk on the Wichita Mountains Wildlife Refuge assuming maximum reproduction and minimum natural loss after 1955.

The outcome of the hypothetical simulation led to two basic conclusions. First, it is my firm belief that there were substantially greater numbers of elk on the Wichita refuge (or adjacent to it) during the 1950's and 1960's than what field counts show. Second, it is also my conclusion that the demographic parameters synthesized and used in the above historical simulations are essentially correct. The fact that the simulations yielded calf totals substantially larger than the reported number during the period 1956 through 1972 can be explained in that the simulations applied an accurate calving rate to a larger population than that upon which reported calf crops were based.

White-tailed Deer Simulations

White-tailed deer, like elk, are secretive animals and many of the difficulties associated with data collection for elk also pose problems in the case of white-tailed deer. Therefore, refuge personnel have come to rely upon similar data-gathering techniques for both species. For example, whereas the elk population is censused by helicopter flights over known elk concentration areas, white-tailed deer are counted by means of roadside inventories in areas of high deer activity. A second similarity involves the way in which reproductive estimates are made. Natality estimates for both white-tailed deer and elk are derived from early fall herd classification checks, although elk natality estimates are currently supplemented with pregnancy data obtained from cows shot during harvest.

Similarities in data-gathering procedures have led in turn to similarities in data bases for the two species. One similarity in the respective data bases involves total population estimates. While Bartnicki (1969) questioned the accuracy of some past elk population estimates, similar reservations should be expressed about the accuracy of previous deer population estimates because of the large multipliers often used to convert actual deer sightings into total refuge population estimates. As one example, 31 deer sighted on the refuge in 1959 led to the conclusion that the refuge population contained 1717 deer (Halloran 1959a).

Most of the demographic information used in the following simulations for white-tailed deer came from the refuge biologist's "Special Report" series which addresses specific topics as population census and trapping records. Those reports date back only to 1955. Therefore, the simulations cover only the period 1955 through 1972.

White-tailed Deer Simulation Results
1955 Through 1963

Of the four ungulate species inhabiting the Wichita rangelands, field data for white-tailed deer are the most incomplete. It was impossible to compare simulation results with many real-world population parameters because the field data needed for those comparisons were not available. Thus, the simulation strategy used for the following deer simulations was simple and consisted of two steps:

(1) annual harvests and reproductive estimates were input to the simulation program as reported and (2) natural mortality (chiefly fawn mortality) was adjusted as necessary to best align simulated population size and trend with corresponding refuge data. The alignment achieved with that strategy must be considered crude at best.

The demographic conditions synthesized directly from refuge reports produced the simulated population trend shown in Fig. 37. Although the simulated and reported population trends show general agreement to the early 1960's, the simulated population began to increase once annual harvesting ceased in 1964.

Least-squares regression tests performed upon fawn:doe ratios compiled between 1963 and 1967 indicated deer reproduction decreased markedly over what it had been during the 1950's. Those lowered reproductive rates were not in use in the simulation shown in Fig. 37. Thus, the fact that the simulated population trend (without reproductive-rate modifications) differed so greatly from actual population trend supported the conclusion that either (or both) reproductive or mortality rates changed in the real population during the 1960's, thereby lowering recruitment and causing the population to decline.

White-tailed Deer Simulation Results
1964 Through 1972

The simulation shown in Fig. 37 was updated to include the lower reproductive rates after 1963 and the resulting simulated

Figure 37. Comparison of reported and simulated population trend for white-tailed deer on the Wichita Mountains Wildlife Refuge based upon reproductive information collected between 1955 and 1961 and an annual population mortality of 6 percent.

population size and trend aligned more closely with reported population information (Fig. 38). But it was apparent that some conditions in the simulated population were still wrong because the simulated population stabilized at about 800 animals whereas the real population is known to have declined to about 500 animals.

The simulation in Fig. 38 was based on force-fit values for population size, reproductive rates and total annual harvest. Thus, mortality rates as the only remaining variable seemed most likely to be wrong. Additional support for selecting mortality as the incorrect variable was found in work reported by Teer et al (1965). Drought conditions existed on the Wichita during the mid-1960's and Teer's group found substantially higher mortality of white-tailed deer during drought years over non-drought years in Texas.

A crude alignment between reported and simulated population size and trend was finally achieved through a series of simulations in which fawn mortality (June through September) was gradually increased. Summer fawn mortality was increased because various persons working on the refuge have observed heavy fawn losses within a few weeks of birth during recent years (Steele 1969; E. A. Bartnicki, personal communication). The best alignment achievable (Fig. 39) was attained with a fawn mortality of 60 percent between June and September and an overall herd annual mortality of 20 percent.
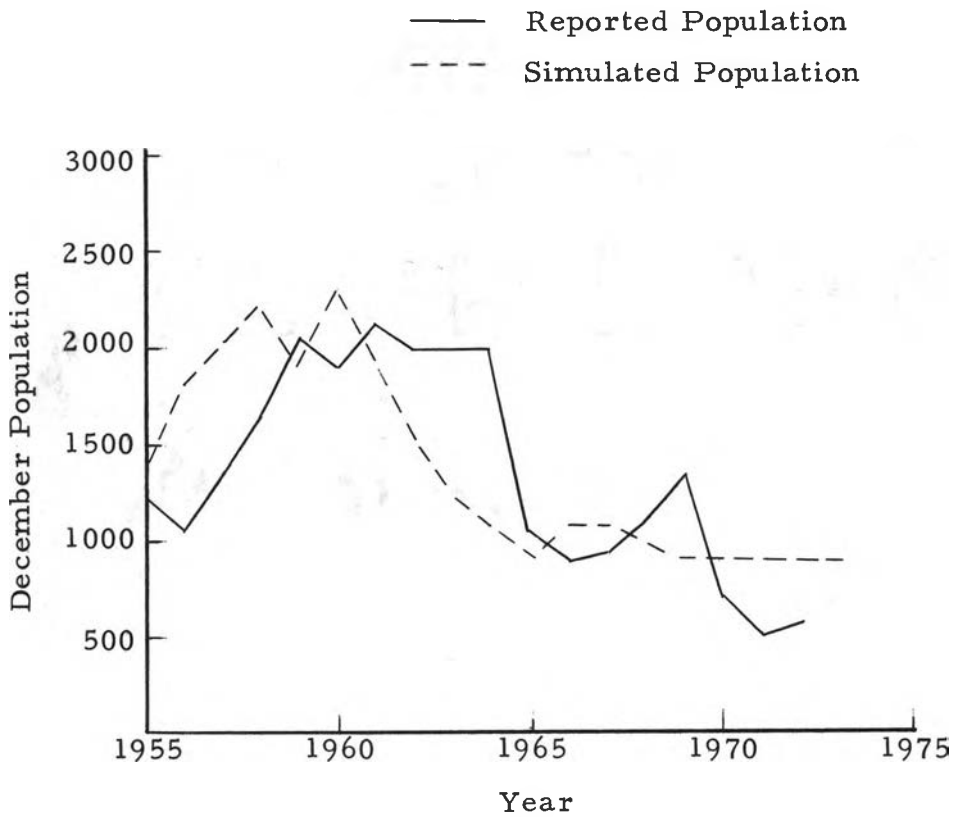
Figure 38. Comparison of reported and simulated population trend for white-tailed deer on the Wichita Mountains Wildlife Refuge updated with reproductive information collected between 1963 and 1972 and an annual population mortality of 6 percent.
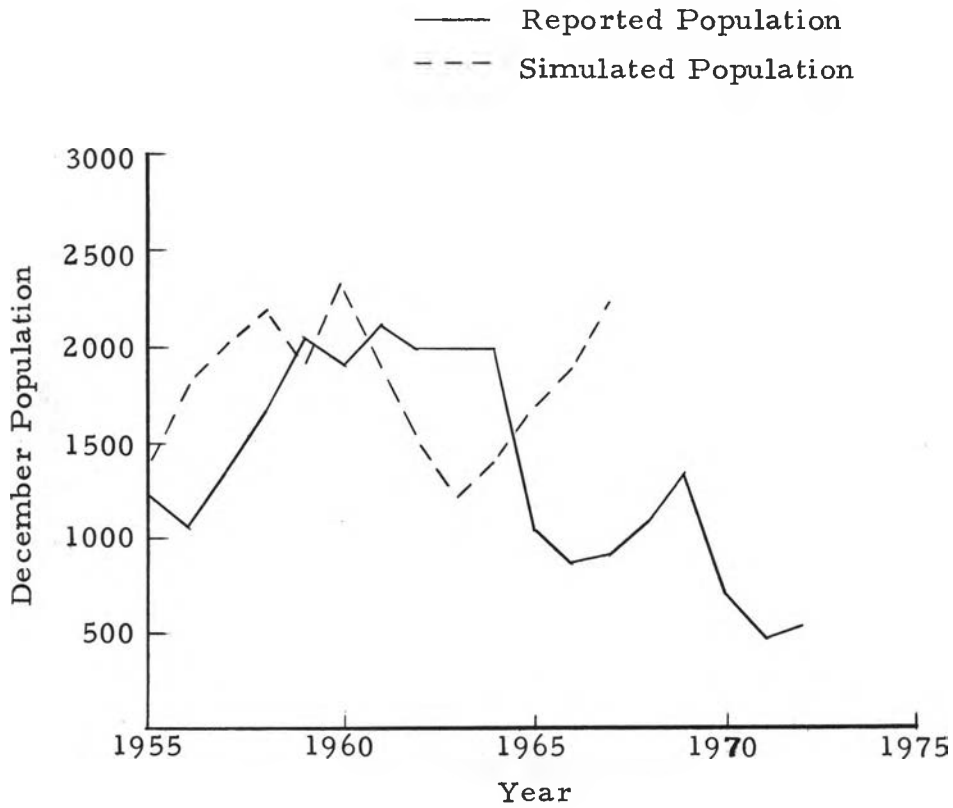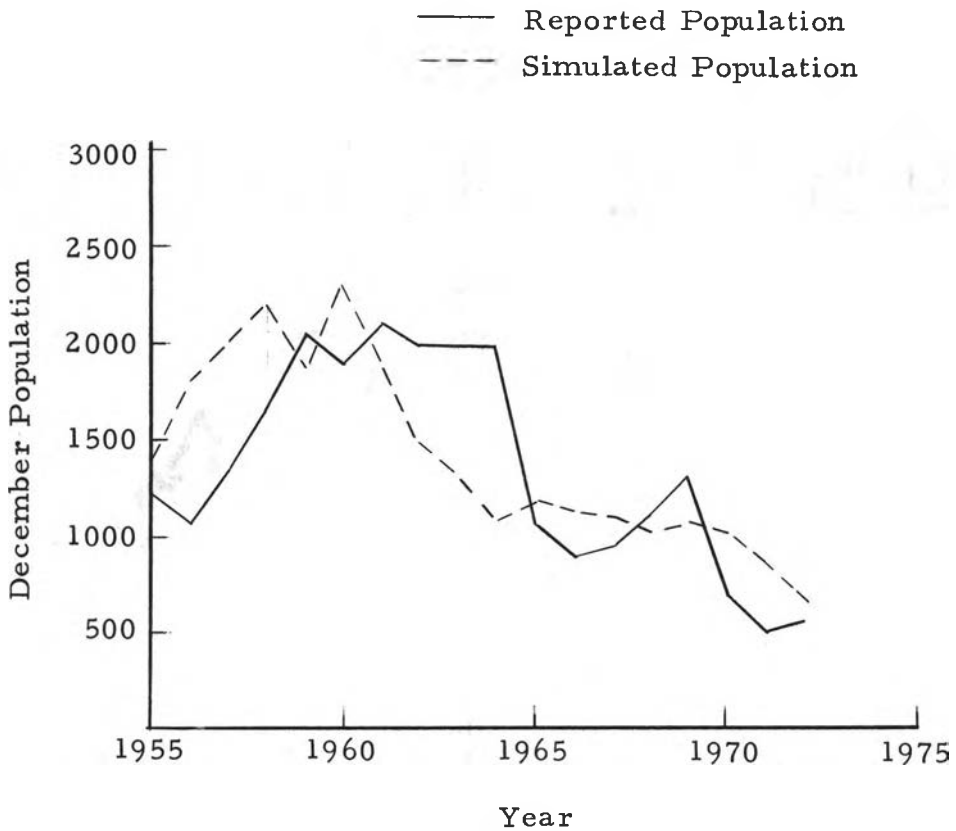
Figure 39. Comparison of reported and simulated population trend for white-tailed deer on the Wichita Mountains Wildlife Refuge updated with reproductive information collected between 1963 and 1972 and 60 percent fawn mortality between June and September.

The white-tailed deer simulations described above actually "forced things to fit" in the sense that natural mortality rates were adjusted to whatever values yielded the simulated population trend which best agreed with reported information. It is unfortunate that that had to be the case because, in the absence of more reliable and complete demographic data, the simulations are limited in their analysis of historic herd biology and thus in their ability to project future population trends and act as a useful management tool.

But another important element which decreases the simulations' usefulness results from habitat conditions on the refuge. Indications are that white-tailed deer habitats on the refuge (as of 1971) have not fully recovered from the drought during the 1960's. The 1971 Wichita range-use check determined that browse stands on the refuge still had not recovered from the severe hedging which occurred when browse production was low and that high browse lines occurred in most wooded areas. Since historic habitat changes apparently brought about demographic changes, habitat recovery in the future is likely to affect reproductive and mortality rates in the deer population. Without knowing in advance what those demographic changes will be, simulations could not do a very precise job of forecasting population trends.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This chapter reflects upon the validity of Program ONEPOP in light of what has been learned about the population biology and management of the big game herds residing on the Wichita refuge. The evaluation derives from examining the program in terms of its compatibility with the mechanisms operating within the Wichita herds and its ability to reproduce herd dynamics over time. In addition, some comments have been made concerning the overall quality and usefulness of the simulations and management implications derived from those simulations.

Technical Validity of Program ONEPOP

Compatibility with Population Mechanisms

A computer model can act as a surrogate for a real-world population only to the extent that it reproduces the mechanisms operating within that population. Thus, it seemed appropriate in a validation analysis to first examine Program ONEPOP in terms of the mechanisms which appeared to be operating in the Wichita herds.

Population Control. Population control is a central feature of population ecology. In essence population control is the mechanism that keeps populations from increasing to infinity or decreasing to

zero. For a simulation model to approach biological reality, it must contain some element of a population-controlling mechanism.

Population ecologists are far from agreement on the mechanisms that control populations. Andrewartha and Birch (1954) believe that populations are not controlled but rather are "limited" by the amount of time during which environmental conditions are suitable for growth. They maintain that populations grow during the time ecological conditions are favorable but decline during periods of unfavorable conditions. In essence, they maintain that limitation (or control) is brought about by factors external to the population. Conversely, Lack (1955), Wynne-Edwards (1962), and Milne (1957) believe control is achieved through processes and mechanisms internal to the population.

Although population ecologists cannot agree on the processes by which populations are limited or controlled, they do agree that populations are controlled in some manner. Obviously populations do not grow to infinitely large numbers nor do they become extinct very often (barring intervention by mankind). Typically populations fluctuate over time between upper and lower limits believed to be ultimately imposed by environmental conditions. This implies that a "linkage" of some sort must occur between the habitat and the population dependent upon that habitat.

Program ONEPOP was realistic with respect to the population controlling mechanism that appeared to link habitat conditions to big game populations on the Wichita refuge. In Program ONEPOP, the assumption was made that reproductive rates are density dependent, i. e., that the linkage between habitat and population occurs through the reproductive process. No evidence was found during the Wichita study which would refute that assumption. Typically reproductive rates for the herds on the refuge exhibited a definite inverse relationship with respect to population density, the only exception being during periods of changing range conditions which does not invalidate density dependent control.

Sex and Age Variations. Populations are not homogenous units but instead are made up of individuals of different sex and age. Basic population theory teaches that individuals of different sex and age often behave differently under similar ecological conditions. For example, prime-age females are more likely to reproduce than are younger females and, even if young females do reproduce, they typically have a lower reproductive rate than the older females. This kind of age-specific reproduction occurred on the Wichita where 2-year-old elk and bison cows reproduced sporadically whereas older females were more consistent from year to year in bearing offspring. A population model can be realistic only to the extent that it can accommodate sex- and age-specific differences in demography and Program ONEPOP provided that capability.

With respect to natural mortality, Program ONEPOP provided for the population to be divided into as many as 20 age classes, with separate mortality rates for each. That capability was not used to fullest advantage, however, during the Wichita study. Theoretically at least, each sex and age class should have mortality rates somewhat different from the others. But, because the Wichita field data were not adequate to permit the calculation of a mortality rate for each age class, the populations were simulated with only four different mortality rates, those for (1) young-of-the-year, (2) yearlings, (3) prime-age adults, and (4) very-old adults. It might be argued then, that since separate mortality rates for all 20 age classes could not be calculated, that the program contained unnecessary detail and should have been modified to reflect a population with only four age categories. This was clearly not desirable because, if for no other reason, the number of animals in each of the 20 simulated age classes was an important piece of information used in alighing the reported and simulated populations. If the reported and simulated number of animals in all age classes closely agreed, one could be reasonably confident that other simulated parameters as sex and age structure of the harvest were also being simulated correctly.

With respect to reproduction, Program ONEPOP recognized only three age classifications: (1) young-of-the year, (2) yearlings, and (3) adults. Thus, all adult age classes were assumed to

reproduce at the same rate. This was perhaps unrealistic because, in theory, some females would not reproduce or would reproduce at a lower rate once they attained a certain age. Whereas the formulation of the program may have been somewhat unrealistic from a biological point of view, it was nevertheless consistent with the way reproductive information has been reported on the Wichita. Typically, all females age 3 years and older have been included in the calculations of reproductive rates and it has not been possible to determine from those field data at what age females become less fertile.

Model Precision and Realism

Precision is the only one of Holling's (1966) suggested validation components which lends itself to quantitative evaluation and was discussed in preceding sections where correlation coefficients were calculated for several population parameters. But the realism of Program ONEPOP has not been dealt with to this point although inferences have been made.

Realism reflects the ability of a simulation model to provide insight into the behavior of the essential features being modeled when they function together as a system. Perhaps the most clearcut example of model realism during the Wichita study was demonstrated in connection with simulations of elk herd history. Program ONEPOP, after integrating several essential features dealing with mortality, harvest, and reproduction, brought to light the fact that

the system could not behave as reported unless there were substantially more elk in the population than reported. It is unlikely that that information would have been uncovered had the herd not been simulated.

Program ONEPOP Simulations as an
Aid to Herd Management

Because of Program ONEPOP's realism and precision, the simulations completed for each herd on the Wichita can serve as a powerful analytical tool in the management of that species in at least two respects. First, the simulations can act as a cross-check, or in a certain sense, a "validation" of the field data gathered on the herd over the years by taking numerous pieces of field data, integrating them into a rigorous system and determining whether or not they account for the dynamics of the herd observed over time. When one or more pieces of information is incorrect, the program cannot reproduce herd history to the extent that those data are in error. The simulations are also an analytical aid in that numerous demographic parameters, such as age ratio of the population or sex structure of the harvest, for which information might not otherwise be available can be estimated. The approximation of missing population parameters is possible only because of the realism with which the simulation combines information on known population parameters.

A second, and perhaps more important benefit the simulations provide for management, is that they represent a device with which the manager can explore various questions he might have concerning herd dynamics. His questions might be entirely theoretical or very pragmatic. For example, the manager might wish to theorize about the effects of future catastrophies in the herd such as epizootics; or he might wish to obtain an early assessment of the consequences and trade-offs associated with some recent decisions about harvest strategy. Some implications for the management of Wichita bison and elk arising from the simulations of those herds are presented below.

Management Implications for Wichita Bison

During a meeting on the refuge in 1974 to discuss preliminary simulations with the refuge staff, the staff indicated that management policy for bison on the Wichita at that time was to maintain a base population of about 635 bison with approximately equal numbers of males and females. Ostensibly that number was chosen because it was in keeping with grazing conditions on the area.

Certainly grazing limitations are important range attributes to be considered when deciding herd policy. But there are at least two other factors which should receive consideration to some extent. The first is animal thrift; i.e., there should be some consideration given to the animal's "quality of life" when deciding upon stocking

level. In a certain sense, animal thrift is related to total grazing capacity because if herd level is maintained below grazing capacity, theoretically the animals should receive adequate nutrition and perform well. That is not to say that the refuge staff has ignored animal thrift when setting past stocking policies. Quite the contrary. The numerous reports on animal body weights contained within the refuge's files indicate that the refuge staff has had a keen interest in how well range conditions have satisfied the animal's nutritional requirements. Although body weights are one method of monitoring animal thrift, information compiled during the present study suggests that perhaps a better indicator of animal thrift might be herd calving rate. In this study, analyses of population data have indicated that during periods of high moisture and (presumably) high forage production, bison calving rates increased over those observed during periods of low forage production. Bison calving rates seem to be strongly correlated with nutritional status.

A second factor which should enter into management decisions is the question of public demand for surplus bison. Assuming that the refuge is committed to meeting at least part of the public's demand for bison, then the number of harvestable animals generated through a given stocking policy should receive consideration along with grazing capacity of the range and animal nutritional status. That seems to be the case because a policy statement drafted in 1971

(Anonymous 1971) speculated what the ultimate public demand for

bison from the Wichita might be and how that demand might be met.

It seems evident, then, that bison management on the Wichita

is a complicated task subject to myriad constraints. To provide the

refuge staff with information useful in decision-making about future

stocking policy for bison on the Wichita, a series of "response

surfaces" (described in Appendix B) was generated from the bison

simulations described above. Field data gathered on the herd

between 1968 and 1972, which represented the latest demographic

and ecological conditions, were used to generate the response sur-

faces which were subsequently analyzed to determine the conse-

quences and trade-offs which would have to be considered in decisions

to manipulate the herd to attain various management goals. Four

management alternatives were compared and are summarized in

Table 29. The first management alternative reflects the anticipated

consequences (in terms of grazing pressure, calving rates, sustained

annual harvest and herd sex ratio) of the 1974 herd policy. But the

other alternatives assess trade-offs (differences in population and

grazing conditions) between that particular alternative and the 1974

policy. Trade-offs are shown in parentheses. To illustrate, a

decision to change herd policy from that of 1974 and maximize view-

ing opportunity (maximize population) would have a trade-off with

respect to sustained annual harvest of 52 fewer bison (138 - 86).

Table 29. Consequences associated with various management strategies for bison on the Wichita Mountains Wildlife Refuge. Trade-offs, shown in parentheses, represent the difference between current-policy values and each management alternative.

| Alternative | Management Goal | Base Population | Trade-off | | | |
			A. U. of Grazing	Calves/ 100 Cows	Sustained Annual Harvest	Bulls 100 Cows
1.	Current Policy	635	952	45	138	100
2.	Maximize Viewing Opportunity	900 (+265)	1350 (+398)	31 (-14)	86 (-52)	100 (±0)
3.	Minimize Grazing Pressure	450[1] (-185)	675 (-277)	45 (±0)	112 (-26)	100 (±0)
4.	Maximize Surplus Bison	770 (+135)	1155 (+202)	33 (-12)	170 (+32)	20 (-80)

[1]This population size was assumed necessary to maintain genetic variability in the population.

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Analysis of the response surfaces also reveal that to achieve a rather

small increase in sustained annual harvest, major trade-offs would

have to be made in base population level. Managing the herd for

maximum sustained harvest would require increasing base population

from the 1974-policy level of 635 bison to about 770, an increase in

grazing pressure of about 21 percent. But that same decision would

increase sustained annual harvest by only about 30 animals per year.

Trade-offs connected with minimizing grazing pressure (but still

maintaining herd viability) thereby leading to maximum animal thrift

are shown in management alternative number 3.

Assessment of Alternative Management Strategies for Elk

Management policy for elk on the Wichita seems to focus upon

two basic guidelines: (1) maintain the population at a level below

grazing capacity and (2) maintain a "representative" (pristine) herd

structure. That policy is effectively carried out by maintaining a

base population of 500 elk with a 50:50 herd sex ratio. The policy

guidelines essentially constitute a "preservationist approach" to

management and are in line with a fundamental objective of the

National Wildlife Refuge System which is "To assure the survival in

a natural state of each of this nation's plant and animal species"

(Bureau of Sport Fisheries and Wildlife 1970). But a paradox occurs

when one considers the method used to maintain herd size and

structure.

Sport hunting is the method used to manipulate size and struc-
ture of the elk herd and hunter demand for elk is on the increase.
For example, a statement on management policy drafted in 1971
stated that 4000 applications were received from Oklahoma residents
when public hunting was first announced (presumably in 1969). That
total compares with 6100 applications received in 1973 (R. Johnson,
personal communication). Hunter demand for harvestable elk re-
mains high and, if the past is any indicator of the future, is likely to
increase even higher in future years.

The refuge staff is therefore placed in the difficult situation of
trying to satisfy two opposing groups. If they choose to manage
primarily for the non-consumptive user and provide many animals
for public viewing, they would almost certainly want to adopt a dif-
ferent management strategy than what they would follow if they chose
to maximize for sport hunting. Perhaps an acceptable compromise
would be to maximize the herd's production of trophy animals (a
"trophy" is considered here to be any bull elk at least 5 years of age).
Such a strategy would probably lower total annual harvest and provide
more animals for viewing but would also tend to compensate the
hunter by providing more animals with large antlers.

Obviously the establishment of management objectives for elk
remains for the refuge staff and their supervisors to decide. But
to provide some alternatives those individuals might consider in

setting future elk management objectives, a set of response surfaces (Appendix C) was generated for the Wichita elk herd and analyzed to ascertain the most likely trade-offs associated with attaining various management goals. The response surfaces were based upon demographic data collected since 1969 which represented the latest ecological and demographic conditions. Trade-offs were assessed in terms of what would be produced under current management policies. For example, the values compiled in Table 30 show that if a decision were made to change current policy and manage the herd for maximum sustained harvest, that decision would require increasing the base population from the current base of 500 to 890 for a trade-off (shown in parentheses) of 390 additional elk. But, by the same token, that policy change would also be expected to increase sustained annual harvest from an average of 120 (achievable with current policy) to 220 for a trade-off of 100 additional elk harvested each year.

Herd Simulations -- A Valid Perspective

Several concluding remarks are in order about the herd simulations discussed above. Because of the tremendous amount of material which had to be sifted in order to gather the data for each simulation, errors must exist. In some cases, there were conflicting accounts in the records and incorrect data may have been chosen for use.

Table 30. Consequences associated with various management strategies for elk on the Wichita Mountains Wildlife Refuge. Trade-offs, shown in parentheses, represent the difference in production between each management alternative and current management policy.

Management Alternative	Management Goal	Base Population	A. U. of Grazing	Trophy Harvest[a]	Sustained Annual Harvest	Bulls/ 100 Cows
1.	Current Policy	500	250	14	120	100
2.	Maximize Harvest	890 (+390)	445 (+195)	9 (-5)	220 (+100)	28 (-72)
3.	Maximize Trophy Harvest	890 (+390)	445 (+195)	36 (+22)	143 (+22)	100 (±0)
4.	Maximize Viewing Opportunity	1025 (+525)	512 (+262)	12 (-2)	83 (-37)	100 (±0)

[a] A trophy is considered to be a bull elk at least 5 years old.

Although the herd simulations are referred to as "final" in this paper, they are final only in the sense that they cannot be improved upon with information available. A more realistic evaluation would be to view each simulation as a first approximation and subject to cautions interpretation. As a necessary next step, members of the refuge staff need to closely scrutinize and comment on each simulation, making corrections where needed and updating each as new information becomes available. The point to be kept in mind about the simulations is that they can never behave exactly like the real-world populations. But hopefully they can approximate those real-world populations closely enough to improve upon the decision-making about them. It is with that hope in mind that this work is offered.

SUMMARY

This paper reports the findings of a study conducted on populations of bison (Bison bison), elk (Cervus canadensis), white-tailed deer (Odocoileus virginianus) and Texas longhorn cattle (Bos taurus) inhabiting the Wichita Mountains Wildlife Refuge in southwestern Oklahoma. The study had two basic objectives: (1) to describe the general population biology of each species and the demographic mechanisms through which population changes have occurred and (2) to use the information obtained in validation tests for a simulation model designed to mimic the dynamics of big game grazing systems. The study represented one segment of a comprehensive research project aimed at developing methodologies through which a systems approach to management might be applied in the stewardship of wildlife resources.

Field studies were not conducted during the investigation, other than those routinely carried out on the refuge by members of the refuge staff. The general population biology of each species and the demographic mechanisms of population change were investigated by compiling and analyzing demographic data contained in existing refuge reports and related documents. The simulation model used during the study, Program ONEPOP, was a model of population dynamics which processed reproductive, natural mortality and

harvest information on a sex-and-age class basis. The model assumed a "closed system" in that all changes in population size were assumed to result from changes in reproductive rates, mortality rates or harvest.

Bison, thought to be indigenous to the Wichita Mountains region, were re-established in the area in 1907. The population subsequently increased from 15 animals transplanted in 1907 to a population of about 500 head in 1972. Bison were managed on the refuge in much the same way cattle are managed on western ranches. Cows typically first bred on the refuge at 2 years of age but some have bred as yearlings. Single births were the rule. Bison calving performance has been erratic over time, fluctuating greatly between years. Reported bison calving rates, which averaged 52 calves per 100 cows between 1960 and 1967, were lower than calving rates reported for bison on the National Bison Range in Montana and herds in Nebraska and South Dakota. The lower Wichita rates may reflect habitat conditions on the refuge because bison calving rates, at least on the Wichita, appeared to fluctuate with grazing conditions. There was also evidence that Wichita bison cows produced calves in alternating years which might explain in part why reported calving rates have varied so much between years.

Longhorn cattle were brought to the Wichita refuge in 1927 in a move aimed at preserving the breed in its ancestral form and were

managed in essentially the same manner as bison. Like bison, long-horn were rounded up each fall at which time surplus animals were disposed of and demographic information on the herd was collected.

Longhorn cows are capable of breeding as yearlings but usually are not bred until 2 years old. Habitat conditions for longhorn on the Wichita appear to be excellent, judging from herd performance. The longhorn population increased from 30 head transplanted in 1927 to 300 by the 1950's and has been maintained at that level through annual herd cropping. Longhorn reproductive success has fluctuated over time, paralleling that observed for bison in several respects. A notable difference in reproductive patterns for the two species was that longhorn calving rates, unlike those for bison, remained fairly constant after the 1950's, averaging about 90 calves per 100 cows annually. Natural mortality among Wichita longhorn was light, averaging about 3 percent of the herd each year.

Elk are also indigenous to the Wichita Mountains region but were exterminated in the late 1800's by uncontrolled hunting. The present refuge population was established in 1911 and 1912 when 20 animals obtained from Jackson Hole, Wyoming were released onto the area. The current population, which numbered about 600 elk in the early 1970's, has descended entirely from those 20 elk. Elk management on the refuge bears many similarities with elk manage-ment techniques used elsewhere in western United States. The herd

is counted from helicopter flights in mid-winter and sport hunting

has been used to regulate herd size since 1969. Prior to 1969,

surplus elk were butchered or donated alive.

Prime breeding age for elk on the Wichita appeared to be about

3 years of age. Cows less than 3 years old bred less often on the

Wichita than in other herds but pregnancy rates for cows 3 years of

age and older were comparable with rates reported elsewhere.

There was evidence that reproduction by young cows was increasing,

perhaps in response to a 60 percent herd reduction in the late 1960's.

Most reproductive information available for Wichita elk was in the

form of pregnancy rates for cows shot during the fall harvest. Little

information was available on actual calving rates for the following

year but the information available indicated little prenatal loss. In

most cases, calf:cow ratios observed in the field during August and

September closely approximated pregnancy rates obtained during the

preceding November or December. Natural mortality rates for

Wichita elk were comparable to those of bison, averaging 5 or 6

percent annually.

Unlike elk, white-tailed deer have never been completely

eliminated from the Wichita area. The present population has de-

scended from animals on the area when the refuge was established

in the early 1900's. Deer were managed on the refuge primarily for

public viewing; sport hunting has never been allowed, although

live-trapping was used until 1964 to remove surplus animals. Population growth was reportedly slow throughout much of the refuge's early history but increased during the 1950's, reaching a population peak of about 2100 deer in the early 1960's. During the interval 1955 through 1964, more than 3500 deer were trapped and removed to reduce over-browsing. Deer population level declined throughout the rest of the 1960's, stabilizing at a level of about 500 by the end of the decade.

The average reported fawning rate for deer on the Wichita between 1956 and 1960 was 63 fawns per 100 does. That rate compared with an average of only 37 fawns per 100 does for the period 1968 through 1972. There can be little doubt that low fawning rates contributed to the population decline of the 1960's but there was also field evidence which indicated that poor fawn survival was involved. Observers noted in the late 1960's and early 1970's that fawn:doe ratios declined from nearly 100 fawns per 100 does during June to about 45 fawns per 100 does in September, which indicated a 50 to 60 percent fawn mortality within a few weeks of birth.

The deer decline occurred throughout the surrounding area and was not limited to the Wichita refuge. It appears therefore, that the factors which caused the decline were region-wide. Drought during the 1960's is the most probable cause but cessation of predator-control efforts early in the 1960's may have had some bearing as well.

Big game populations on the Wichita were held at mean density by annual cropping. Mean density for the Wichita herds relates to postharvest population size, however, and therefore does not explain the year-to-year fluctuations in preharvest population size. Factors which might explain fluctuations in preharvest population include (1) movements, (2) changes in death rate and (3) changes in birth rates.

Movements were an unlikely explanation for fluctuations in pre-harvest population size because of fencing which surrounded the refuge and restricted immigration and emigration. Coefficients of determination (r^2) indicated that the two factors which accounted for most of the variation in preharvest population size were harvest rate of the previous year and reproductive rate. Harvest rate can be controlled at the discretion of the refuge staff but herd reproductive rates are influenced to a great extent by environmental conditions. Factors found to have bearing on changes in reproductive rates were: (1) total annual precipitation, (2) food supply, and (3) lactation status of the animal.

The relation between total annual moisture and herd reproductive rate was best illustrated by significant ($p = 0.05$) correlations between bison calving rates and total annual precipitation of the previous year. Elk pregnancy rates were also positively correlated with total annual precipitation, although the relation was not significant at the 5 percent level. Field data suggested that the amount of

moisture received in August and September, immediately prior to and during the elk rutting period, may have exerted greater influence upon elk pregnancy rates than total annual moisture. Events similar to "flushing" in domestic animals occurred in the Wichita elk population during 1969 and 1971, causing a greater percentage of elk cows to become pregnant during those two years than during other years. In 1969 and 1971, the percentage of the annual moisture total received during August and September was well above the long-term average. The hypothesized relation between moisture and reproductive rates was reinforced by findings that significantly ($p = 0.01$) greater numbers of 2-year-old elk cows were pregnant during "wet" years than "dry" years. During years when total annual moisture equaled or exceeded the long-term average amount (wet years) an averaged 58.8 percent of the 2-year-old elk cows examined were pregnant compared to an average 2.8 percent during years received below-average amounts of moisture.

Elk pregnancy rates were not significantly ($p = 0.05$) correlated with estimated forage production on Boulder Ridge and Hilly-Stony range types (suspected elk habitat). Likewise, bison pregnancy rates were not significantly ($p = 0.05$) correlated with estimated forage production on Loamy Bottomland range sites (suspected bison habitat). Trends in pregnancy rates for both species, however, were similar to forage-production trends on the respective areas.

Data gathered on the lactation status of adult cow elk suggested an inverse relation existed between lactation rate and incidence of pregnancy. The pattern was one of rather high incidence of pregnancy and low incidence of lactation in one year followed by the opposite condition the following year.

Findings for the Wichita grazing system support the widely held belief that range condition has a strong bearing upon ungulate reproduction. This appears especially true of range conditions immediately prior to and perhaps during the breeding period. Conditions during that time seem to place limits upon the reproductive level for the Wichita herds in any given year.

Reproduction among wild ungulates, is complex, involving many separate factors which can change from year to year. A conceptual model was developed, showing the suspected relations between basic components of the reproductive process and range variables as they appear to exist on the Wichita refuge.

In validating Program ONEPOP, demographic information abstracted from the refuge files was used to simulate the dynamics of each herd over time. The simulation program was validated from the standpoint of two validation criteria, precision and realism.

Precision is a validation criterion concerned with the ability of a simulation model to generate values for parameters contained within the model which compare with real-world values and can be

quantified with standard statistical tests. The precision with which Program ONEPOP simulated the Wichita populations was ascertained by computing coefficients of determination (r^2 values) between the reported and simulated values of population parameters contained within the model, including those associated with population size and trend, reproduction, and harvest.

Model realism is related to the ability of a model to provide insights into the behavior of the modeled parameters when they function together as a system. Statistical procedures seemed inappropriate for ascertaining the realism of Program ONEPOP and a non-quantitative technique was used. Frequently, when natality and mortality rates synthesized directly from the refuge files were input into Program ONEPOP, the simulated population failed to align with other reported population information (e.g., population size and population trend). If the field data input into the simulation had been correct, there would have been close agreement between all reported and simulated values. Thus, the realism of Program ONEPOP was documented through its ability to demonstrate the mathematical impossibility of certain reported data combinations.

When inaccurate field data were detected, it was possible to continue with the simulation of that particular population only after approximating more nearly correct values for the erroneous (or missing) field data through a process referred to as "data alignment"

which took into account the reliability of the field data. All field data used in the simulation were first ranked according to their relative reliability based upon (1) the quantity of field data available for that parameter and (2) the accuracy of the field techniques used to acquire the information. Data alignment consisted of deciding which piece(s) of field data was least reliable (and therefore most likely wrong) and also how to adjust those data so that they interlocked with other, accurately known pieces of field data.

Field data for longhorn cattle on the refuge were comparatively good but there were deficiencies and omissions. For example, the total number of longhorn removed from the herd annually had been recorded throughout the herd's history. But almost entirely missing from the record were data on the sex and age distribution of the annual removals. Information of that nature dated back only to the mid-1960's and thus had to be approximated for all other years by partitioning the reported total annual harvest (reliable field data) between males and females so as to approximate the reported population sex and age structure (also reliable information) during December following the harvest.

The greatest degree of alignment between reported and simulated information for longhorn cattle was with respect to population size and trend. But simulated population sizes were often 20 to 40 animals greater than corresponding reported values between 1955

and 1972, a result believed due largely to the use of constant repro-
ductive and mortality rates in the simulation during that same period.
Even though there were minor population-size differences, the
simulations were thought to realistically approximate the actual
dynamics of the longhorn population over time.

Similarities in management practices for longhorn cattle and
bison on the refuge have led in turn to similarities in data availability
and data accuracy for the two herds. Taken as a whole, the reported
information for bison was good but some of the data omissions which
characterized the longhorn data base also appeared in the bison field
data. For one thing, total annual harvests had been consistently
reported for both species but little reported information was available
on sex and age structure of the harvest. The similarities in data
availability and accuracy led to the use of similar simulation strate-
gies for the two herds.

Tests of statistical correlation indicated that Program
ONEPOP simulated bison population size and trend, calving rates,
and herd sex structure with high precision. Correlation tests were
not carried out, however, on total annual calf crop and annual harvest
because both of those parameters were set in the bison simulations
to equal actual values and therefore statistical tests were largely
inappropriate.

Elk on the Wichita refuge tend to concentrate in remote sectors of the refuge characterized by dense stands of blackjack oak and steep-to-moderate terrain. The rugged nature of elk habitat makes it difficult to acquire information on the herd and has forced the refuge biologist to rely upon data-gathering techniques which typically lack the directness of the techniques used to obtain information about longhorn cattle and bison. Difficulties connected with data acquisition have led to the reporting of some dubious information for elk, especially information connected with the number of elk on the refuge during any given year.

Population sizes simulated for the Wichita elk population with Program ONEPOP were invariably greater than corresponding reported population sizes. In fact, during part of the 1960's, simulated population sizes were as much as 57 percent greater than the reported population totals. The reported population totals were discredited by statements in the records that the population counts were considered to be "conservative estimates" of the actual refuge population and that elk known to have escaped from the refuge and moved onto adjacent areas were not included in the reported population total. Simulations with Program ONEPOP demonstrated that even if the number of elk suspected of being outside the refuge were added to the reported total, the revised count would have still been much below the actual elk number, providing evidence that the Wichita elk population was underestimated for a number of years.

White-tailed deer, like elk, are secretive animals and many of the difficulties associated with data collection for elk also pose problems in the case of white-tailed. Therefore, refuge personnel have come to rely upon similar data-gathering techniques for both species.

Reported population totals for white-tailed deer were suspect, primarily because of the large multipliers used to convert actual deer sightings into total refuge population estimates. As one example, 31 deer sighted on the refuge in 1959 led to the conclusion that the refuge population contained 1717 deer. Although the reported population totals were questionable, there was reasonably good information on what the population trend had been over time. There was also good information on white-tailed deer removals on the refuge.

Because of a general lack of reliable demographic information, the white-tailed deer simulations actually "forced things to fit" in the sense that natural mortality rates were adjusted to whatever values yielded the simulated population trend which best agreed with reported information. It is unfortunate that that had to be the case because, in the absence of reliable and complete demographic information, the simulations were limited in their analysis of historic herd biology and thus in their ability to project future population trends and act as a useful management tool.

Results obtained during the investigation indicate that Program ONEPOP is realistic with respect to the demographic mechanisms operating within the Wichita herds. Population ecologist agree that wild populations are controlled through some linkage between habitat conditions and the population, although they have not agreed on what mechanisms are involved. Program ONEPOP assumes that reproductive rates are density-dependent, i.e., that the linkage between habitat and population occurs through the reproductive process. No evidence was found during the Wichita study which refuted that assumption.

Program ONEPOP is also compatible with real-world population structures. Populations are not homogenous units but instead are made up of individuals of different sex and age. Basic population theory teaches that individuals of different sex and age often behave differently under similar ecological conditions. Program ONEPOP provided for a population to be divided into as many as 20 age classes, with separate mortality rates for each. The program also allowed different reproductive rates to be applied to females of different age groupings.

Because of the realism and precision with which Program ONEPOP simulated the Wichita populations, the simulations can serve as powerful analytical tools in at least two respects. First, the simulations can be used to cross-check the accuracy of field data

collected for each population over time. Second, the simulations can act as devices with which the manager can explore alternative management strategies for each population.

Although the herd simulations are referred to a "final" in this paper, they are final only in the sense that they cannot be improved with information available. As a necessary next step, members of the refuge staff need to closely scrutinize and comment on each simulation, making corrections where needed and updating each as new information becomes available. The simulations can never behave exactly like the real-world populations but hopefully they approximate those real-world populations closely enough to improve upon the decision-making about them.

LITERATURE CITED

Allred, B. W. 1955. Here still is a land primeval. Soil Cons. 20(9): 195-201.

Andrewartha, H. G. and L. C. Birch. 1954. The distribution and abundance of animals. Univ. of Chicago Press, Chicago. 728 pp.

Anonymous. 1914. Chronological summary of the principal items connected with deer on the Wichita N. F. Wichita Mountains Wildlife Refuge Report. 6 pp. (Typewritten)

Anonymous. 1927. Chronological summary of the principal items connected with buffalo on the Wichita N. F. Wichita Mountains Wildlife Refuge Report. 19 pp. (Typewritten)

Anonymous. 1927a. Chronological summary of the principal items connected with deer on the Wichita N. F. Wichita Mountains Wildlife Refuge Report. 6 pp. (Typewritten)

Anonymous. 1930. Chronological summary of the principal items connected with elk on the Wichita N. F. Wichita Mountains Wildlife Refuge Report. 6 pp. (Typewritten)

Anonymous. 1971. (No title). Wichita Mountains Wildlife Refuge Report. 5 pp. (Typewritten)

Barney, L. and R. Cunningham. 1970. Bison in Theodore Roosevelt National Memorial Park. Buffalo Manage. Seminar, Denver, Colo. 10 pp.

Bartnicki, E. A. 1969. 1969 elk calf crop. Wichita Mountains Wildlife Refuge Biological Report No. 2. 2 pp. (Typewritten)

Bartnicki, E. A. 1970. 1969 deer herd classification check. Wichita Mountains Wildlife Refuge Biological Report No. 5. 2 pp. (Typewritten)

Bartnicki, E. A. 1971. Re-evaluation of range carrying capacity; recommendations for stocking. Wichita Mountains Wildlife Refuge Biological Report No. 19. 18 pp. (Typewritten)

Bartnicki, E. A. 1972. Brucellosis in Wichita's big game herds; review and recommendations. Wichita Mountains Wildlife Refuge Biological Report No. 29. 2 pp. (Typewritten)

Bartnicki, E. A. 1972a. Aerial census of elk, March 3 and 7, 1972. Wichita Mountains Wildlife Refuge Biological Report No. 25. 2 pp. (Typewritten)

Bartnicki, E. A. 1973. Wichita elk population -- a glance-to-the-rear, projection, objective level proposed, and recommendations for removal. Wichita Mountains Wildlife Refuge Biological Report No. 34. 3 pp. (Typewritten)

Beasom, S. L. 1974. Relationships between predator removal and white-tailed deer net productivity. J. Wildl. Manage. 38(4): 854-859.

Blair, W. F. and T. H. Hubbell. 1938. The biotic districts of Oklahoma. Am. Midland Nat. 20(2): 425-454.

Bolte, J. R., J. A. Hair and J. Fletcher. 1970. White-tailed deer mortality following tissue destruction by lone star ticks. J. Wildl. Manage. 34(3): 546-552.

Boyd, R. J. 1970. Elk of the White River Plateau, Colorado. Colo. Div. Game, Fish and Parks Tech. Publ. No. 25. 126 pp.

Buck, P. 1964. Relationships of the woody vegetation of the Wichita Mountains Wildlife Refuge to geological formations and soil types. Ecology 45(2): 336-344.

Buechner, H. K. and C. V. Swanson. 1955. Increased natality resulting from lowered population density among elk in southeastern Washington. No. Am. Wildl. Conf., Trans. 20: 560-567.

Bureau of Sport Fisheries and Wildlife. 1970. National wildlife refuge objectives handbook. U.S. Department of the Interior. 86 pp.

Cheatum, E. L. and J. E. Gaab. 1952. Productivity of north Yellowstone elk as indicated by ovary analysis. Ann. Conf. West. Assoc. Game and Fish Comm., Proc. 32. 174-177.

Churchman, C. W. 1968. The systems approach. Dell Publishing Co., N. Y. 243 pp.

Crockett, J. J. 1964. Influence of soils and parent materials on grasslands of the Wichita Mountains Wildlife Refuge, Oklahoma. Ecology 45(2): 326-335.

Draper, N. R. and H. Smith. 1966. Applied regression analysis. John Wiley and Sons, Inc. New York. 407 pp.

Edwards, R. Y. and R. W. Ritcey. 1958. Reproduction in a moose population. J. Wildl. Manage. 22(3): 261-268.

Flook, D. R. 1970. Causes and implications of an observed sex differential in the survival of wapiti. Canadian Wildl. Ser. Report Series, No. 11. 71 pp.

Follis, T. B. and J. J. Spillett. 1974. Winter pregnancy rates and subsequent fall cow/calf ratios in elk. J. Wildl. Manage. 38(4): 789-791.

Forrester, J. W. 1961. Industrial Dynamics. M.I.T. Press.

Greer, K. R. 1966. Fertility rates of the northern Yellowstone elk population. Ann. Conf. West. Assoc. Game and Fish Comm., Proc. 46: 123-128.

Gross, J. E., J. E. Roelle and G. L. Williams. 1973. Program ONEPOP and information processor: a systems modeling and communications project. Colo. Coop. Wildl. Res. Unit, Colo. St. Univ. 327 pp. (Mimeo)

Halloran, A. F. 1956. Buffalo facts from the Wichita. Wichita Mountains Wildlife Refuge Special Report No. 30. 4 pp. (Typewritten)

Halloran, A. F. 1956a. Record data on Wichita longhorn -- 1955. Wichita Mountains Wildlife Refuge Special Report No. 32. 2 pp. (Typewritten)

Halloran, A. F. 1956b. Coyote-deer relationships on the Wichita. Wichita Mountains Wildlife Refuge Special Report No. 34. 4 pp. (Typewritten)

Halloran, A. F. 1957. Wichita elk weights. Wichita Mountains Wildlife Refuge Special Report No. 46. 3 pp. (Typewritten)

Halloran, A. F. 1958. Winter elk census and supplementary data: 1958-1959. Wichita Mountains Wildlife Refuge Special Report No. 61. 6 pp. (Typewritten)

Halloran, A. F. 1959. 1959 Wichita deer census. Wichita Mountains Wildlife Refuge Special Report No. 63. 2 pp. (Typewritten)

Halloran, A. F. 1960. Wichita buffalo notes, a progress report. Wichita Mountains Wildlife Refuge Special Report No. 79. 16 pp. (Typewritten)

Halloran, A. F. 1960a. 1960 winter elk census, helicopter and ground. Wichita Mountains Wildlife Refuge Special Report No. 70. 2 pp. (Typewritten)

Halloran, A. F. 1961. Progress report, May 1-15. 1961. Wichita Mountains Wildlife Refuge Memorandum No. 133. 1 p. (Typewritten)

Halloran, A. F. 1962. Additional longhorn cattle management records from Wichita Mountains Wildlife Refuge. Okla. Acad. Sci., Proc. 42: 268-271.

Halloran, A. F. 1963. History of the Wichita Mountains Wildlife Refuge elk herd. Okla. Acad. Sci., Proc. 43: 299-232.

Halloran, A. F. 1964. Wichita biological survey -- 64 years in review. Wichita Mountains Wildlife Refuge Report. 45 pp.

Halloran, A. F. 1967. Progress report-Wichita bison productivity study. Wichita Mountains Wildlife Refuge Special Report No. 169. 5 pp. (Typewritten)

Halloran, A. F. and B. P. Glass. 1959. The carnivores and ungulates of the Wichita Mountains Wildlife Refuge, Oklahoma. J. Mammal. 40(3): 360-370.

Halloran, A. F. and C. A. Shrader. 1960. Longhorn cattle management on Wichita Mountains Wildlife Refuge. J. Wildl. Manage. 24(2): 191-196.

Haugen, A. O. 1974. Reproduction in the plains bison. Iowa St. Journal of Res. 49(1): 1-8.

Herman, C. M. 1945. Some worm parasites of deer in California. Calif. Fish and Game 31(4): 201-208.

Hickey, J. J. 1974. Some historical phases in wildlife conservation. Wildl. Soc. Bull. 2(4): 164-170.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memoirs Entomol. Soc. Canada. 48: 1-86.

Kimball, J. F. Jr. and M. L. Wolfe. 1974. Population analysis of a northern Utah elk herd. J. Wildl. Manage. 38(2): 161-174.

Kingery, C. E. 1966. Report of annual range utilization check. Wichita Mountains Wildlife Refuge Report. 3 pp.

Knight, R. R. 1970. The Sun River elk herd. Wildl. Mono. 23: 66 pp.

Lack, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 pp.

Lee, C. 1973. Models in planning. Pergamon Press, New York. 142 pp.

Leopold, A. 1933. Game management. Charles Scribner's Sons, N. Y. 481 pp.

Maynard, L. A. and J. K. Loosli. 1969. Animal nutrition. McGraw-Hill Book Co., N. Y. 613 pp.

Milne, A. 1957. The natural control of insect populations. Canadian Entomologist. 89(5): 193-213.

Morrison, E. B. 1950. Feeds and feeding. Morrison Publ. Co., Ithaca, N. Y. 1207 pp.

Moustgaard, J. 1969. Nutritive influences upon reproduction. p. 489-516. In: Cole, H. H. and P. T. Cupps (eds.). Reproduction in domestic animals. Academic Press, N. Y. 657 pp.

Ransom, A. B. 1967. Reproductive biology of white-tailed deer in Manitoba. J. Wildl. Manage. 31(1): 114-123.

Roelle, J. E. 1971. Refuge management modeling (National Bison Range). Colo. Coop. Wildl. Res. Unit Quart. Rept. 25(2): 19-23. (Mimeo)

Rohlf, F. J. and R. R. Sokal. 1969. Statistical tables. W. H. Freeman and Co., San Francisco. 253 pp.

Severinghaus, C. W. and E. L. Cheatum. 1965. Life and times of the white-tailed deer. p. 57-259. In: Taylor, W. P. (ed). The deer of North America. Stackpole Co., Harrisburg, Pa. and the Wildl. Manage. Inst., Wash., D. C. 688 pp.

Simkin, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 29(4): 740-750.

Steele, J. L. Jr. 1968. Investigation of Comanche County deer herd. Job Completion Report, Okla. Dept. Wildl. Cons. Project W-87-R-2. 8 pp. (Typewritten)

Steele, J. L. Jr. 1969. An investigation of the Comanche County deer herd. Final Report. Okla. Dept. Wildl. Cons. Project W-87-R-8. 20 pp. (Typewritten)

Steele, J. L. Jr. 1969a. Investigation of Comanche County deer herd. Job completion report, Okla. Dept. Wildl. Cons. Project W-87-R-a. 9 pp. (Typewritten)

Teer, J. G., J. W. Thomas and E. A. Walker. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildl. Mon. 15: 62 pp.

Verme, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage. 33(4): 881-887.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior. Oliver and Boyd, Edinburgh. 653 pp.

Zimmerman, D. R., H. G. Spies, H. L. Self and L. E. Casida. 1960. Ovulation rate in swine as affected by increased intake just prior to ovulation. J. Animal Sci. 19(1): 295-301.

Some Birds and Mammals Common to the

Wichita Mountains Wildlife Refuge

Species included are according to checklists provided by

Halloran (1964).

Birds

Pied-billed grebe (Podilymbus podiceps)
Great blue heron (Ardea herodias)
Ring-necked duck (Aythya collaris)
American wigeon (Anas americana)
Redhead (Aythya americana)
Red-tailed hawk (Buteo jamaicensis)
Marsh hawk (Circus cyaneus)
American kestrel (Falco sparverius)
Bobwhite (Colinus virginianus)
Turkey (Meleagris gallopavo)
Killdeer (Charadrius vociferus)
Screech owl (Otus asio)
Great horned owl (Bubo virginianus)
Chuck-will's widow (Caprimulgus carolinensis)
Common flicker (Colaptes auratus)
Red-bellied woodpecker (Centurus carolinus)
Scissor-tailed flycatcher (Muscivora forficata)
Eastern phoebe (Sayornis phoebe)
Horned lark (Eremophila alpestris)
Barn swallow (Hirundo rustica)
Blue jay (Cyanocitta cristata)
Crow (Corvus brachyrhynchos)
Carolina chickadee (Parus carolinensis)
White-breasted nuthatch (Sitta carolinensis)
Bewick's wren (Thryomanes bewickii)
Eastern bluebird (Sialia sialis)
Eastern meadowlark (Sturnella magna)
Red-winged blackbird (Agelaius phoeniceus)
Summer tanager (Piranga rubra)
Cardinal (Richmondena cardinalis)
Rufous-crowned sparrow (Aimophila ruficeps)
Lark sparrow (Chondestes grammacus)

Mammals

Opossum (Didelphis marsupialis)
Shorttail shrew (Blarina brevicauda)
Least shrew (Cryptotis parva)
Eastern mole (Scalopus aquaticus)
Cave myotis (Myotis velifer)
Western pipistrel (Pipistrellus hesperus)
Western big-eared bat (Corynorthinus plecotus)
Blacktail jackrabbit (Lepus californicus)
Eastern cottontail (Sylvilagus floridanus)
Desert cottontail (Sylvilagus audubonii)
Blacktail prairie dog (Cynomys ludovicianus)
Eastern fox squirrel (Sciurus niger)
Hispid pocket mouse (Perognathus hispidus)
Plains harvest mouse (Reithrodontomys montanus)
Deer mouse (Peromyscus maniculatus)
Brush mouse (Peromyscus boylii)
Hispid cotton rat (Sigmodon hispidus)
Eastern Woodrat (Neotoma floridana)
Norway rat (Rattus norvegicus)
Coyote (Canis latrans)
Grey fox (Urocyon cinereoargenteus)
Raccoon (Procyon lotor)
Striped skunk (Mephitis mephitis)
Bobcat (Lynx rufus)
Elk (Cervus elaphus)
White-tailed deer (Odocoileus virginianus)
Texas longhorn cattle (Bos taurus)
Bison (Bison bison)

Response Surfaces for

Wichita Bison

Theory

As discussed in previous sections, the primary function of Program ONEPOP is to analyze and duplicate as closely as possible the demographic conditions which have brought a particular population to its current status. If we assume that basic ecological conditions (e. g., range conditions) remain fairly constant in the future, the potential outputs from a population can be ascertained from response surfaces developed in the following manner.

Density-dependent reproduction seems to occur in all of the Wichita big game herds; there is a tendency for the number of young per female to decline as breeding herd size increases. Under the influence of such reproductive rates, a population will stabilize at a particular density if a given mortality rate is consistently applied over time. The population will stabilize at that density where reproduction exactly offsets losses from all forms of mortality. But in addition to a characteristic density, the stabilized population will also have a characteristic calf crop, sex structure, age structure and will also yield a characteristic annual harvest on a sustained basis.

The response surfaces shown on the following pages in essence summarize the results of numerous computer simulations in which

the Wichita bison population was artificially stabilized by varying two

harvest (mortality) parameters, total annual harvest and sex ratio

in the harvest. For example, there was one series of simulations in

which only male bison were harvested and harvest rate was incre-

mented from 0.0 to 1.0. That series of simulations was followed by

a second series in which 10 percent of the bison harvested were

females, with harvest rate again systematically incremented from

0.0 to 1.0. By systematically increasing the percentage of females

in the harvest from 0 to 100 percent, all possible harvest alterna-

tives were simulated. The values for individual population parame-

ters (population size, calf crop, total annual harvest, etc.)

corresponding to each combination of harvest rate and sex ratio in

the harvest were plotted to create the various response surfaces.

Interpretation

The lines which make up the following response surfaces are

similar to the contour lines on a topographic map. All points along

any given contour line have the same value. Thus we can trace along

a particular contour line and determine what combinations of harvest

rate and sex ratio in the harvest will produce the same level of out-

put. Or, as a second approach, we can locate a particular X and Y

coordinate and read from the contour lines the level of output corre-

sponding with that particular harvest strategy. By locating that same

X and Y coordinate on the other response surfaces, we can determine

how that harvest strategy will affect other population parameters.
For example, we might first pick the harvest strategy that maxi-
mizes harvest, and observe on a second response surface what post-
harvest population size would be. Through the use of these response
surfaces, it is therefore possible to explore the trade-offs associated
with various harvest strategies, and it is this capability that was
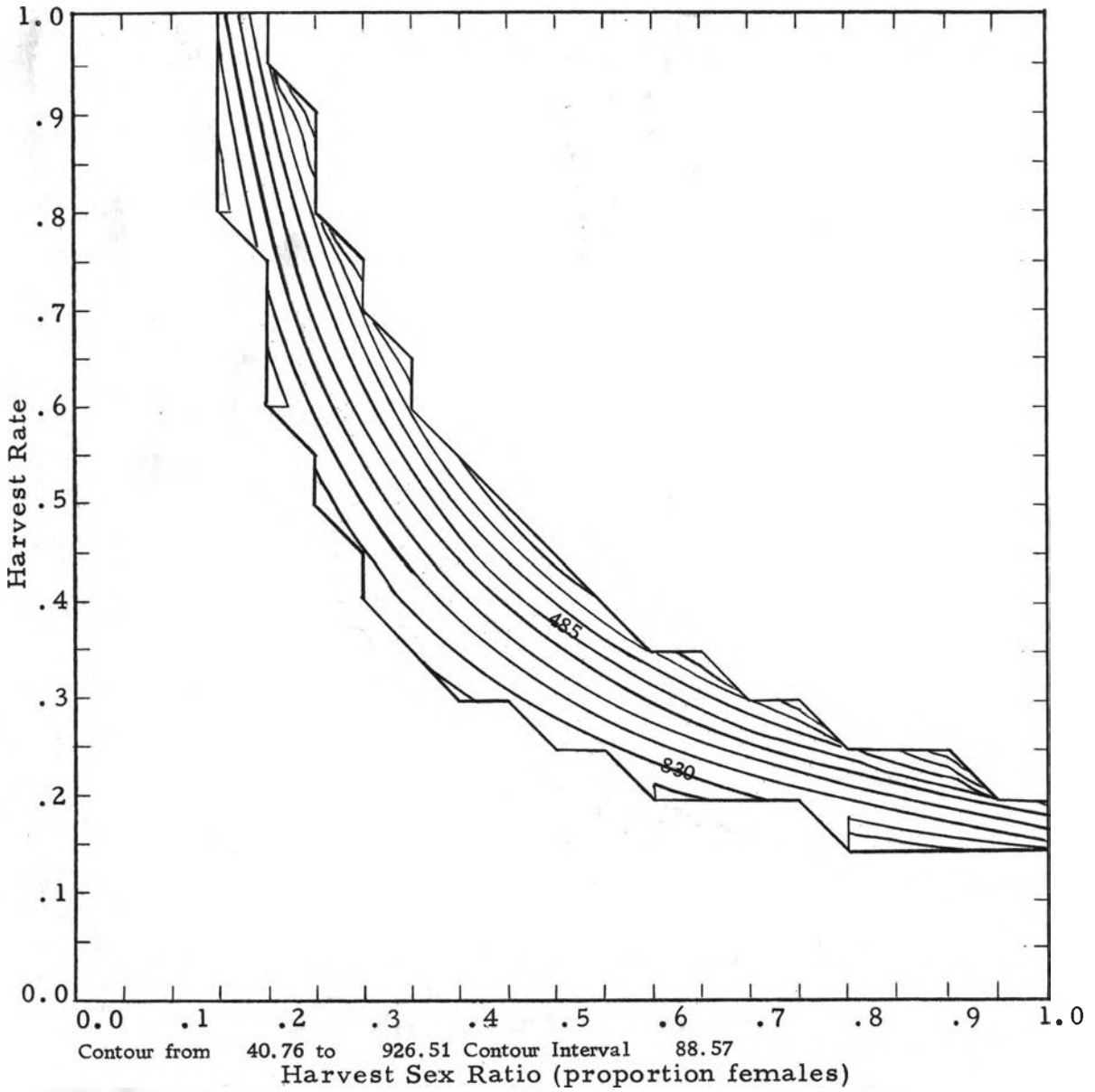used to provide the information on alternative management strategies
for bison listed in Table 31.

Figure 40. Response surface of postharvest population size for bison on the Wichita Mountains Wildlife Refuge.

Contour from   5.94 to   169.72 Contour Interval   16.38
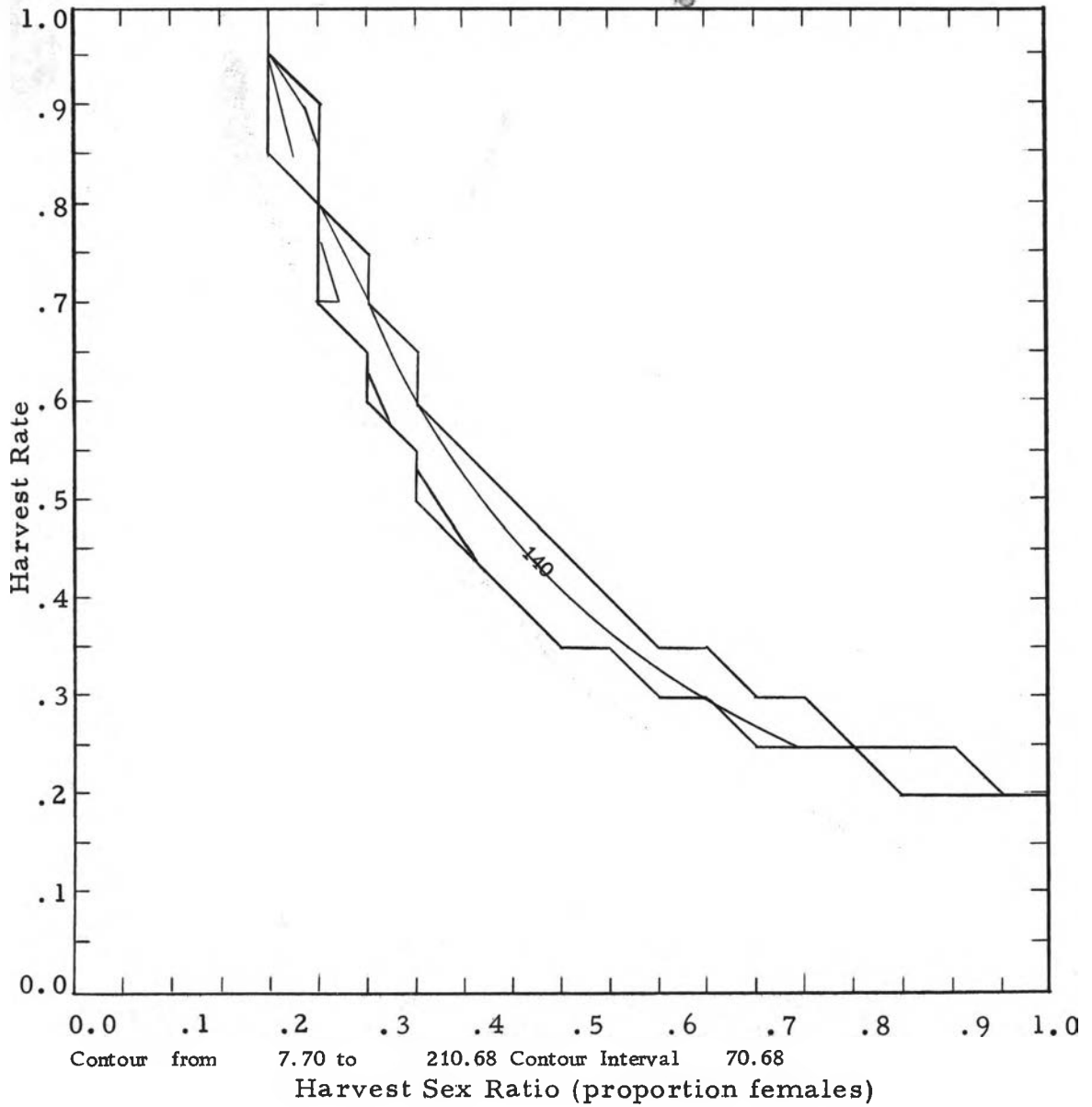
Harvest Sex Ratio (proportion females)
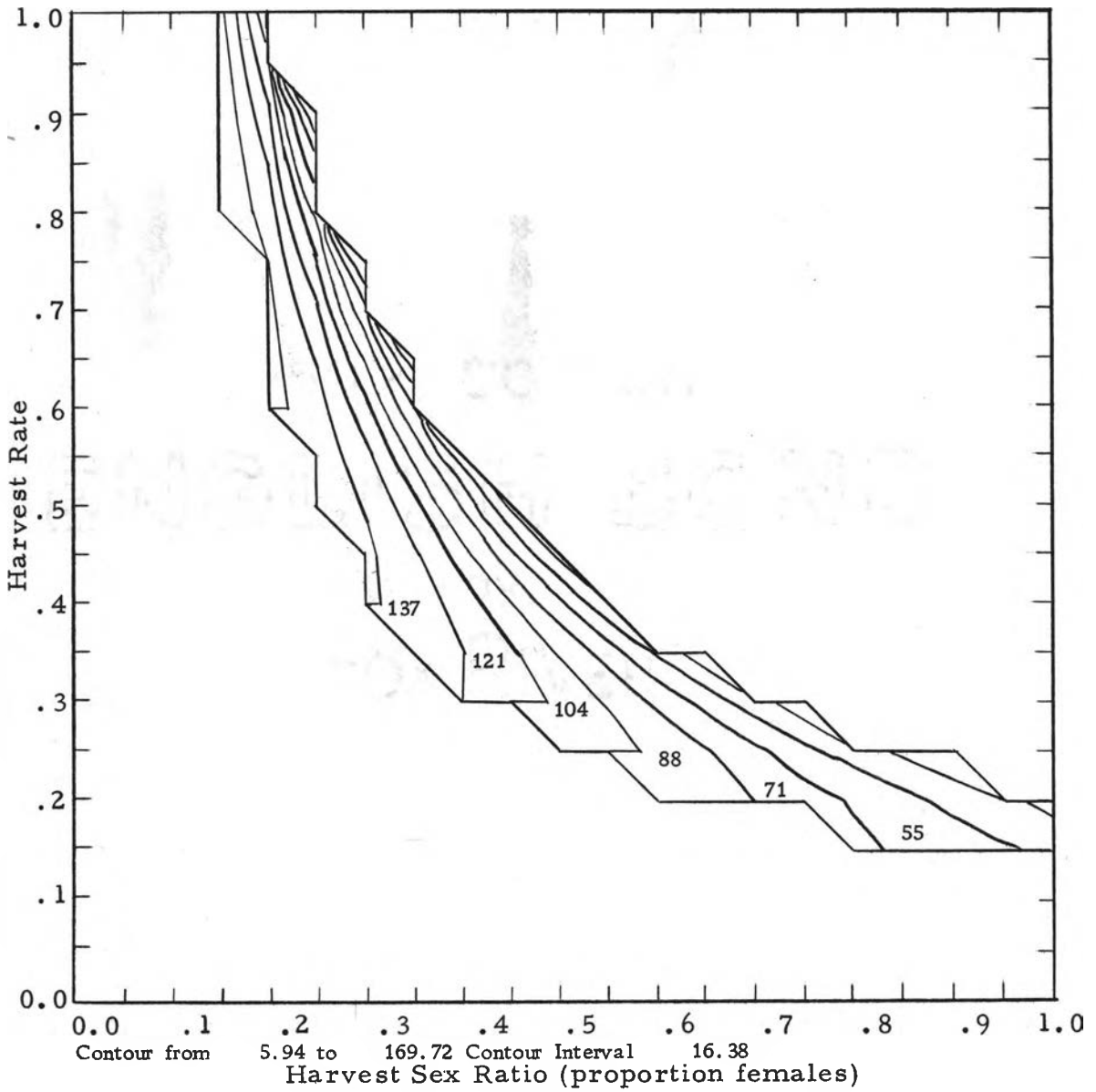
Figure 41. Response surface of sustained annual yield for bison on the Wichita Mountains Wildlife Refuge.
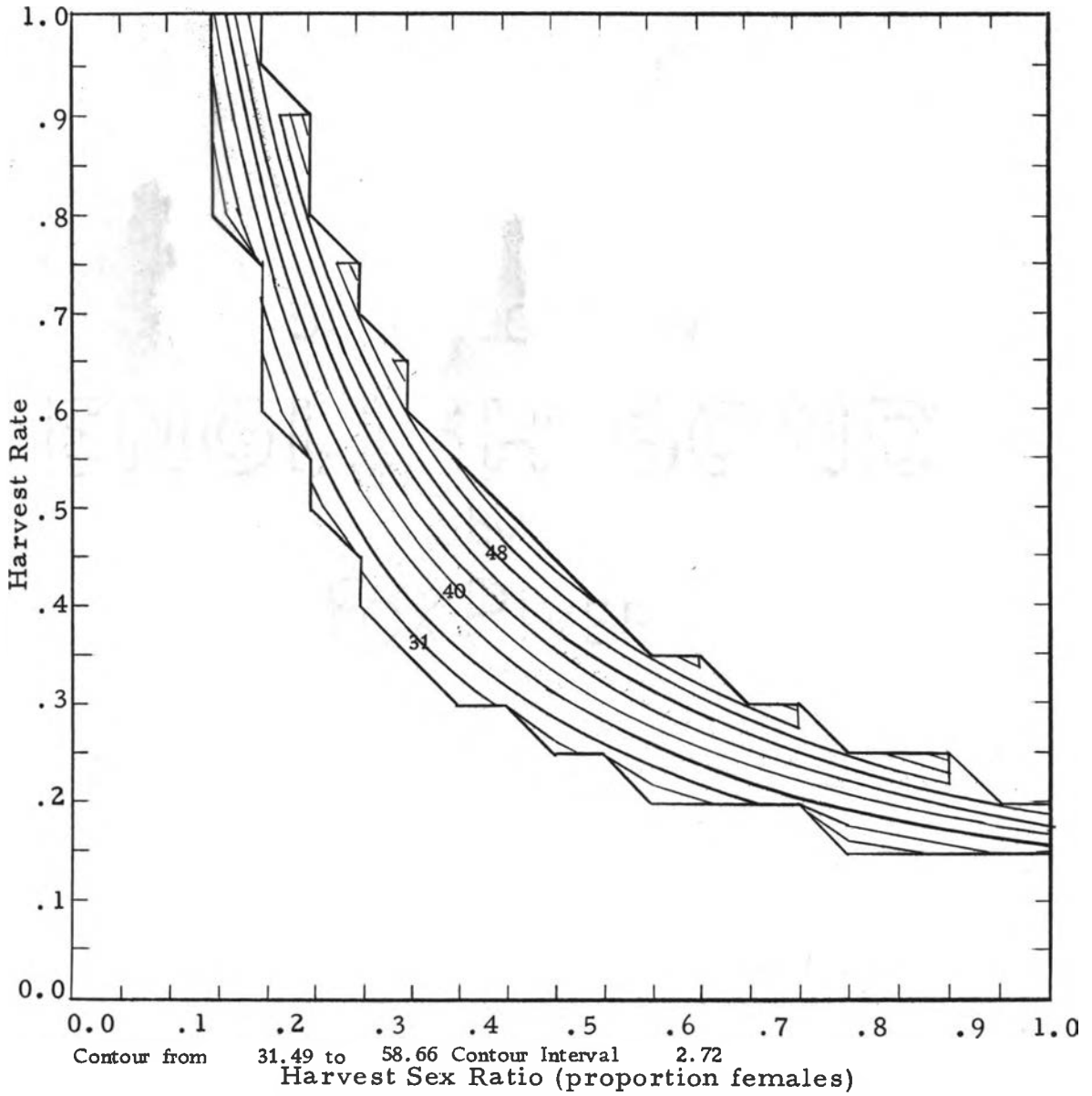
Figure 42. Response surface of calves per 100 cows for bison on the Wichita Mountains Wildlife Refuge.
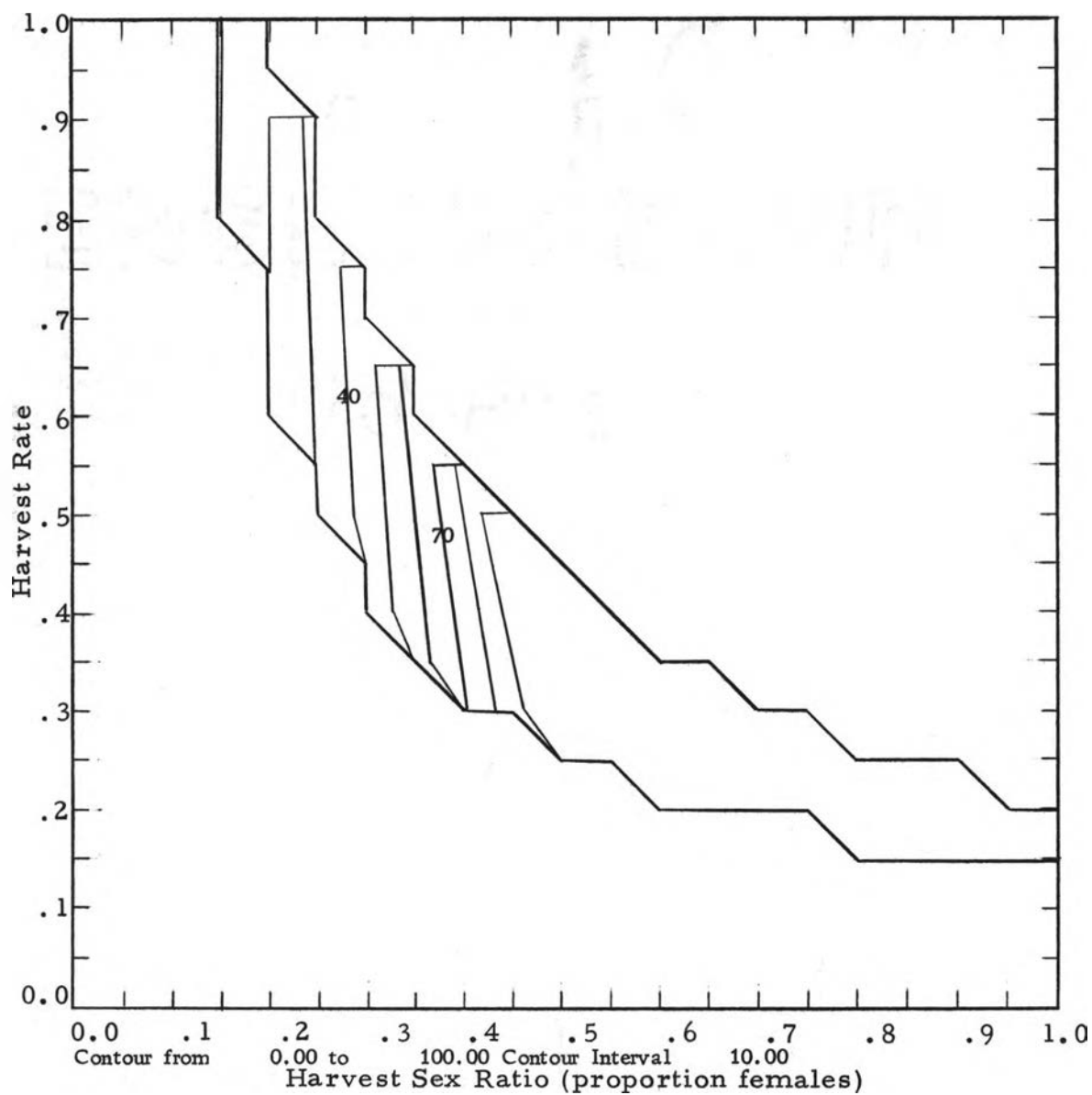
Figure 43. Response surface of bulls per 100 cows for bison on the Wichita Mountains Wildlife Refuge.

Response Surfaces for

Wichita Elk

The following response surfaces for elk on the Wichita Mountains Wildlife Refuge were produced in the same manner as those described for bison. Reproductive and natural mortality rates used in the creation of the response surfaces represent herd conditions between 1969 and 1972.
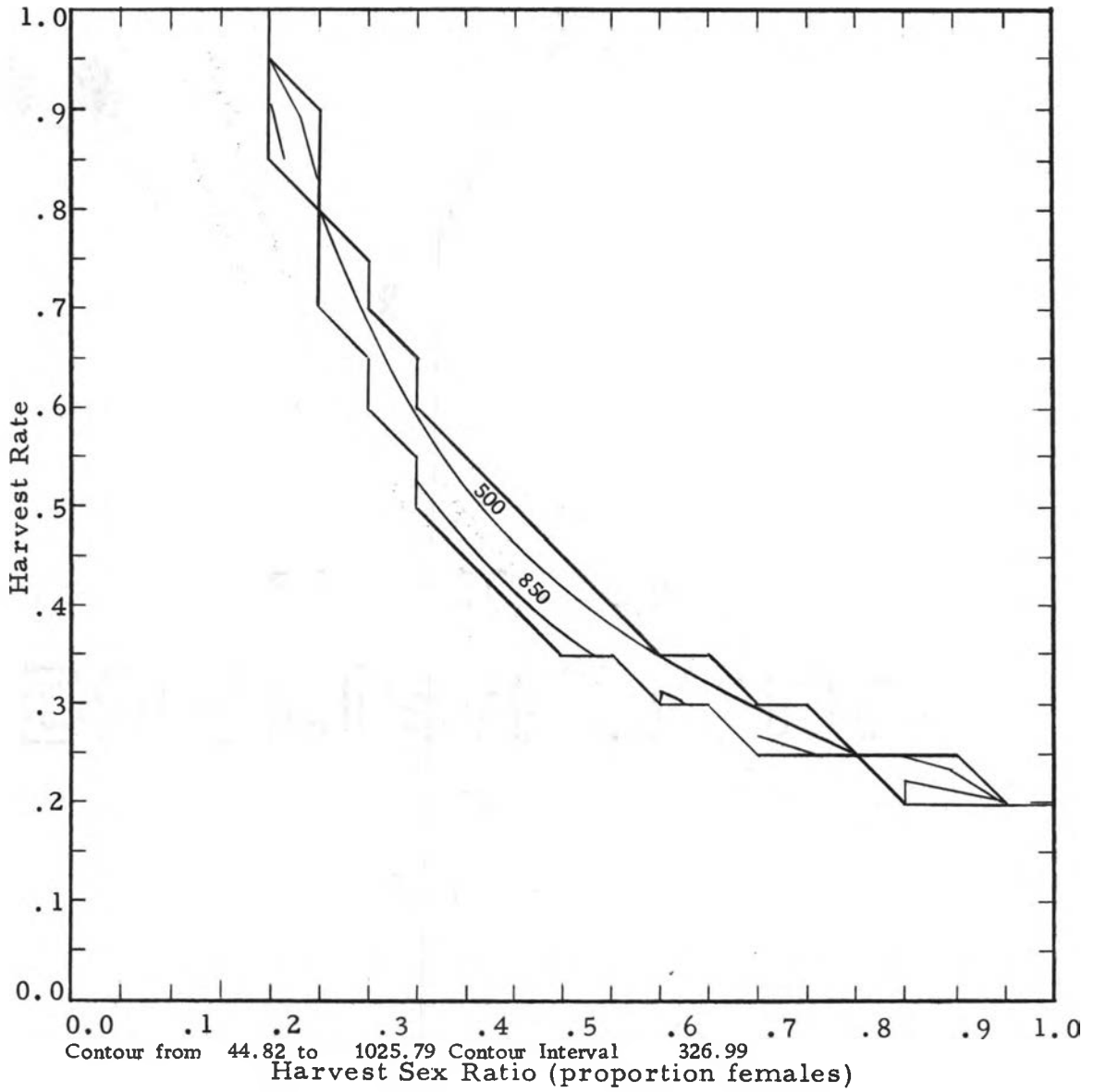
Figure 44. Response surface of postharvest population size for elk on the Wichita Mountains Wildlife Refuge.

Figure 45. Response surface of sustained annual yield for elk on the
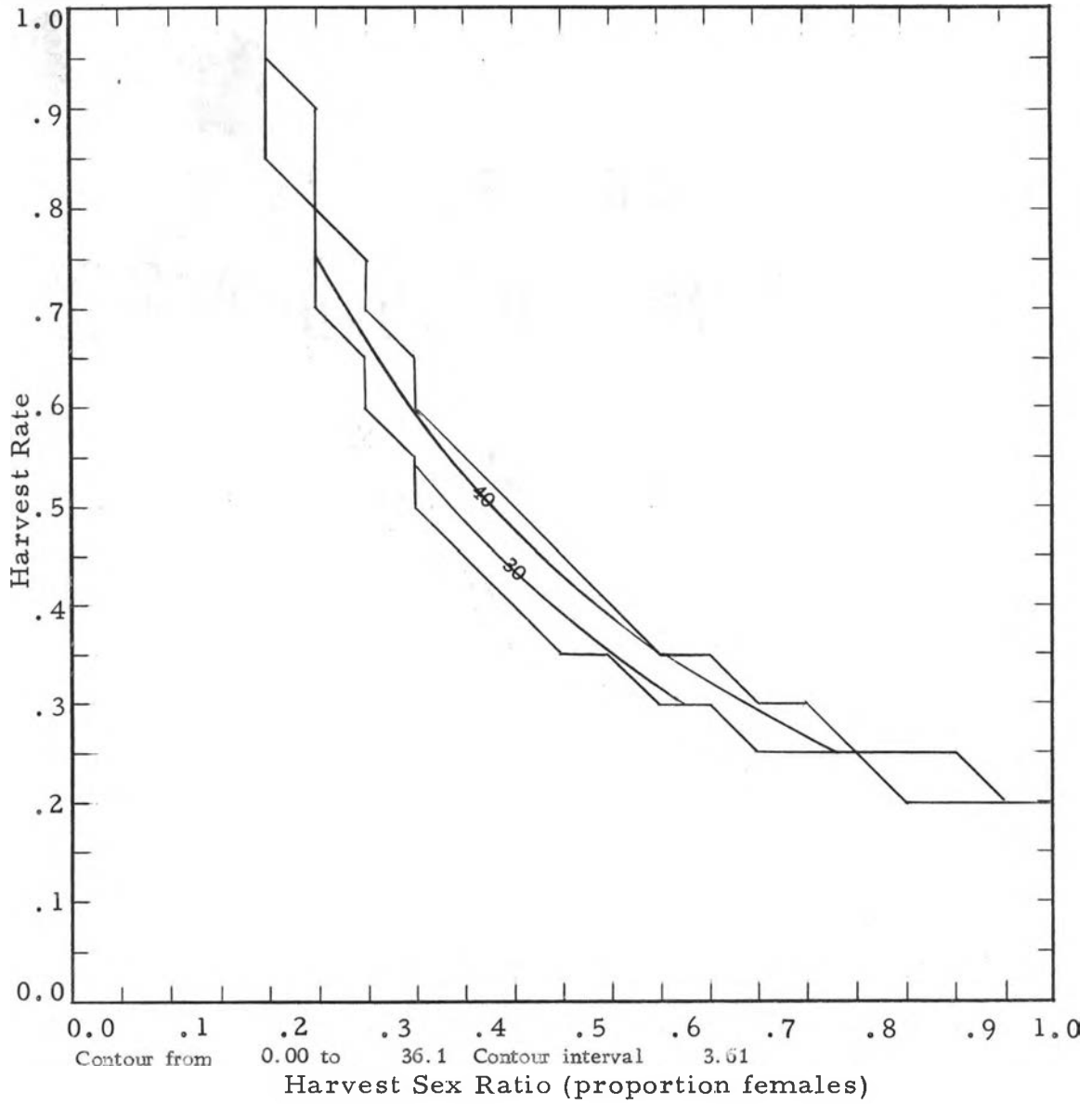Wichita Mountains Wildlife Refuge.

Figure 46. Response surface of annual trophy harvest for elk on the Wichita Mountains Wildlife Refuge.
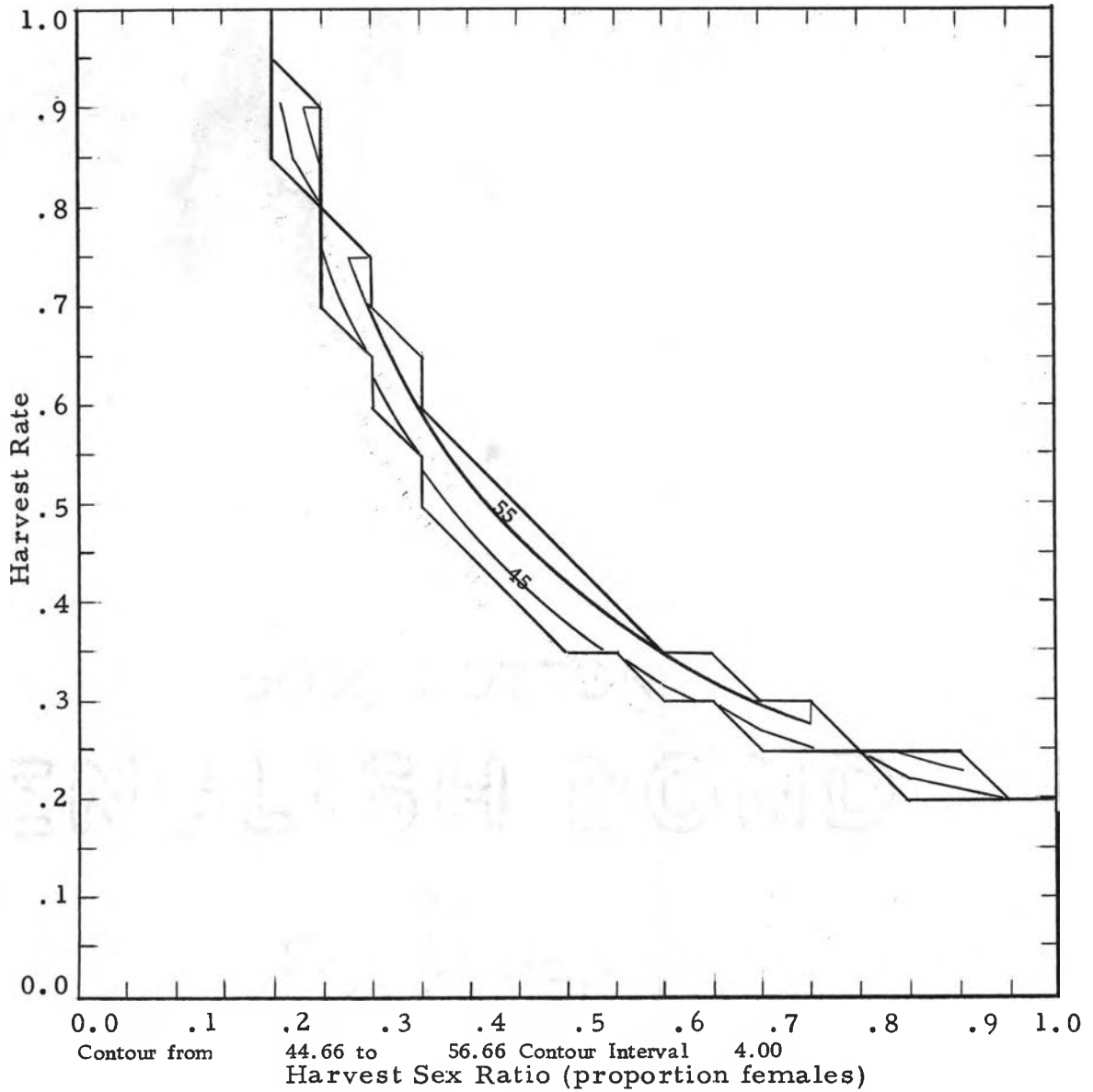
Figure 47. Response surface of calves per 100 cows for elk on the Wichita Mountains Wildlife Refuge.
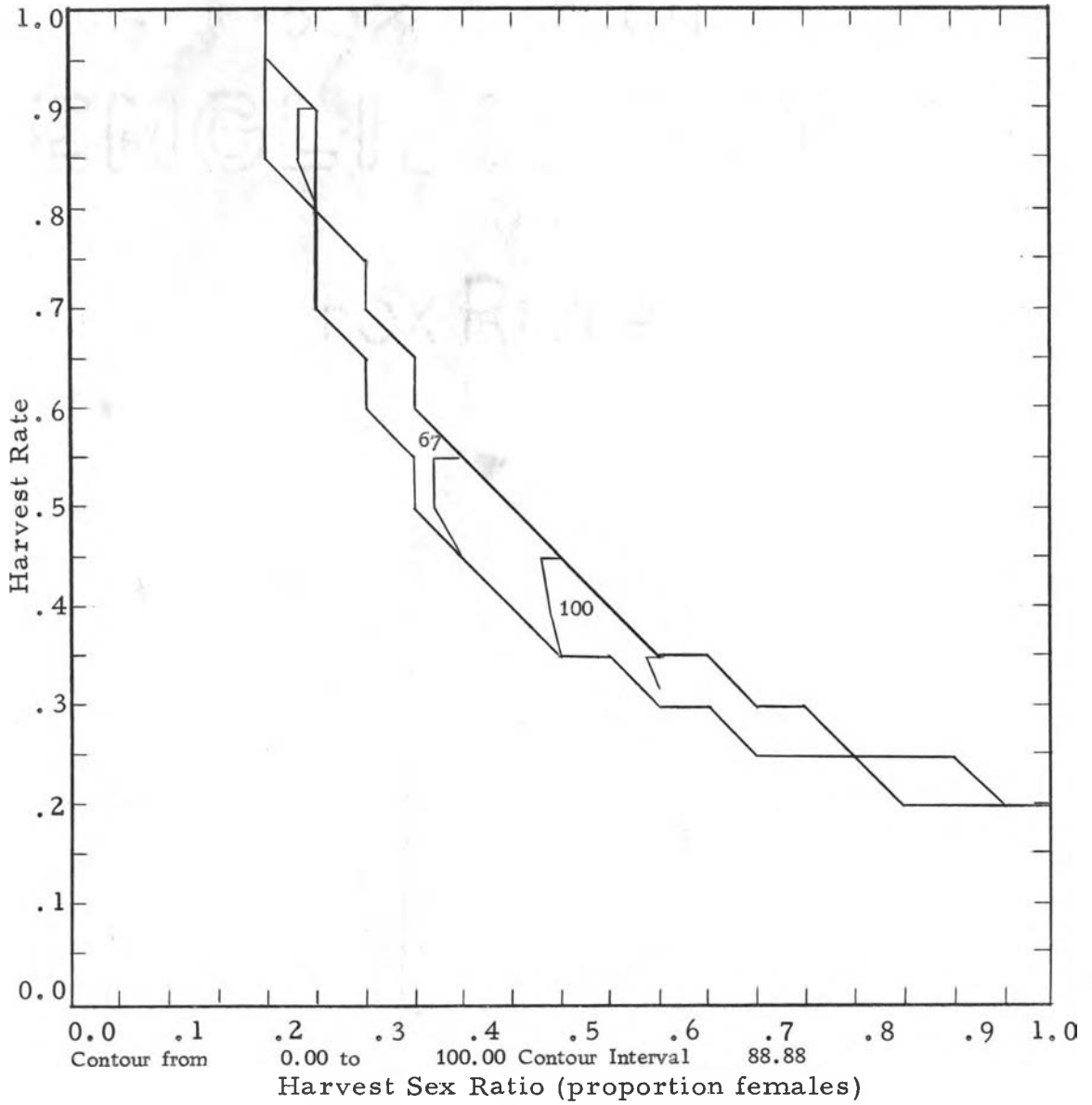
Figure 48. Response surface of bulls per 100 cows for elk on the
Wichita Mountains Wildlife Refuge.