A Computer Simulation Study of Deer in Mendocino County, California

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I. INTRODUCTION

Deer (*Odocoileus* spp.) have long been ranked as the number one big game animal in North America, not only in terms of their abundance, but from the standpoint of hunting interest as well. A recent survey indicated approximately 10 million deer in the 48 contiguous states plus some 3.7 million deer in Canada and Alaska (Longhurst, 1957). At least six million hunters pursue deer each year in the United States.

Along with the general trend in outdoor recreational activities, the number of deer hunters in California increased from 124,000 in 1930 to about 449,000 in 1956, the peak year. Currently the number of hunters is about 390,000. By 1980 it is expected that there will be 525,000 deer hunters in California (California Fish and Game Commission, 1966). But this increased demand will be accompanied by a variety of human encroachments into rural lands, resulting not only in decreased deer habitat but also in less land open to deer hunting.

The human population in California is expected to increase from 19.9 million in 1970 to 28 million by 1980 (California State Office of Planning, 1968). By 1980, a half million acres of rural land is expected to be occupied by urban and industrial expansion. This will result in firearms restrictions for health and safety reasons. Parts of Los Angeles County have been closed to hunting with firearms for many years and additional closures may be expected as urbanization proceeds.

After reviewing these conflicting trends, the California Fish and Game Commission (1966) predicted a 16 percent decrease from the present 50 million acres of big game hunting lands and a 25 percent increase in the number of deer hunters by 1980. To accommodate the additional hunters more intensive wildlife management will be needed on those lands where hunting will continue. One such area is Mendocino County.

In terms of numbers of deer taken, Mendocino County is historically the leading deer hunting county in California. Located approximately 90 miles north of San Francisco, Mendocino County includes 3,510 square miles of diverse habitat types. As elsewhere in California, future changes in land use will cause alterations of deer habitat (Table 1). Nevertheless, the area will continue to support a large deer population for the foresee-

Table 1. Vegetation types in Mendocino County, California[1]

Types	Acreage 1963	Percent of county	Acreage 1980 (projected)	Percent of county
Redwood	667,000	29.7	680,000	30.1
Coastal forest	339,000	15.1	310,000	13.8
Pine-fir-chaparral	200,000	8.9	196,000	8.7
Minor conifer	31,000	1.4	31,000	1.4
Hardwood	133,000	5.9	111,500	5.0
Woodland-chaparral	99,000	4.4	100,000	4.5
Woodland-grass	239,020	10.6	191,820	8.5
Chaparral	163,000	7.3	154,000	6.9
Coast sagebrush	4,000	0.2	4,000	0.2
Grassland	297,425	13.2	356,609	15.9
Agriculture	35,795	1.6	40,411	1.8
Urban-industrial	9,500	0.4	13,000	0.6
Lakes, bays, reservoirs	5,960	0.3	32,860	1.5
Riparian	400	trace	400	trace
Barren	22,300	1.0	24,800	1.1
Total	2,246,400	100.0	2,246,400	100.0

[1] California Fish and Game Commission (1966: 882).

able future. Numerous management problems and economic values are associated with deer in Mendocino County and the potential benefits of improved management are great, not only because of the large numbers of deer, but because of the proximity of the county to a large number of hunters in the San Francisco Bay area. These considerations, together with the research experience of the authors on deer in the area, led to the selection of Mendocino County as the site for this study.

Wildlife Management

Wildlife management attempts to direct a complex, dynamic biosystem toward certain objectives. The components of a wildlife management system include: (1) a well-defined set of policy objectives for the resource; (2) knowledge of the significant interactions between the population of interest and the habitat, and between the population of interest and other animal populations, both domestic and wild; (3) the ability to tailor regulations and their enforcement to the management strategies which will move the biosystem toward satisfaction of the objectives, and (4) a means of monitoring the response of the biosystem to various management strategies.

Policy objectives

The following set of deer management objectives was adopted by the California Fish and Game Commission on February 2, 1968.

1. Produce and maintain a maximum breeding stock of deer on all lands of California, public or private, suitable as deer habitat and consistent with local forage conditions and other uses of such lands. Utilize through public hunting the available crop of deer produced annually by this breeding stock and all surplus animals, of either sex, over and beyond what the range can carry in a healthy condition.
2. Maintain for deer the best possible range conditions consistent with other uses, improve deer ranges which are open to public hunting, and encourage private landowners or tenants to improve their deer ranges even though hunting is limited.
3. Keep deer populations in balance with local forage supplies and conflicting uses, and manage deer herds on the basis of natural forage without recourse to artificial feeding.
4. Subject to the policy on Depredation, . . . control populations of deer which are damaging land or property by regulated public hunting whenever possible, otherwise by permit shooting.
5. The demands of deer shall have priority over other big game species, native or introduced, whenever conflicts arise over the allocation of forage.
6. Regulate the number of deer predators on the basis of local deer needs, particularly on understocked ranges or ranges where hunters are fully harvesting the annual deer crop.
7. Make objective surveys of the deer herds annually and report the results to the Commission as soon as they are compiled.

Biological information

Deer exist within complex biosystems. A biosystem is a group of physical components connected or related in such a way as to form and/or act as an entire unit with a purpose. Deer interact with their habitat, compete with other animals, are affected by diseases and predators, and can increase or decrease in response to intentional or unintentional changes in the habitat. The general attributes of good or poor deer habitats in California have been documented (Longhurst et al., 1952; Taber and Dasmann, 1958), and deer population trends in specific areas can often be predicted from land use patterns, particularly those which affect vegetation. Logging, grazing, farming, and other economic pursuits have great influence on deer numbers, but game managers rarely have control over such activities. Fires on wildland often play a major role in changing deer food supplies. Deer thrive best on successional stages of vegetation and, in general, any management which replaces climax with subclimax vegetation tends to improve range conditions for deer. Additionally, climatic variations have both direct and indirect effects on deer numbers. Despite their obvious importance, however, only a few quantitative estimates of deer population responses to land use and climatic changes in California are available.

Hunting regulations

Regulations have been used to restrict the utilization of various wildlife species throughout wildlife management history (Leopold, 1933). Important components of the regulation-setting process include deer densities, hunter success (in previous years), the recommendations of special interests such as hunters, recreationists, landowners, and anti-hunting groups, and the management policy objectives for the wildlife resource.

Since the deer belong to the people of the state collectively, deer management responsibility is vested in the legislature, which delegates specific regulatory functions to the Fish and Game Commission and the director of the Department of Fish and Game, both appointed by the governor. The commission makes policy for the Fish and Game Department. Management recommendations adhere to these policies but are also influenced by field data gathered by department employees. In setting hunting regulations, the commission frequently departs from department recommendations after receiving recommendations from the general public. Thus, political considerations also play a part in the regulation-setting process.

One factor which complicates the establishment of deer management regulations is the ownership pattern of the habitat. Although deer are public property, much of the habitat is owned by private parties who often regard the deer as an economic liability.

Monitoring the biosystem

To effectively manage a wildlife species such as deer, a routine data collection procedure is needed to monitor the responses of the system to changes in habitat, weather, competition, and hunting regulations.

Deer populations are characterized by potentially high birth and death rates, that is, high rates of turnover. Given the appropriate sets of physical and biological conditions, populations can increase or decrease explosively. Unless the monitoring procedures are sensitive to all significant changes in the population size and composition and can gauge the relation between the population and habitat and other important features of the biosystem, management and regulations cannot hope to move the population toward the objectives in an effective manner.

At present, the deer in Mendocino County are monitored by collection of statistics on the hunting kill and by herd composition counts in spring and fall. In addition, some carcass transects are run annually to gain a relative index of winter losses, and data are collected on the number of deer killed on the highways by motor vehicles.

An important shortcoming of the present monitoring system is its failure to distinguish the effects of hunting on deer populations from other (uncontrolled) effects resulting from land use or climatic variations. Current monitoring efforts also fail to elucidate many details of deer population dynamics. In particular, the magnitude of changes in reproduction and survival due to variations in weather phenomena and consequent forage production cannot be fully assessed by fragmentary studies.

Biomanagement Models

Wildlife management has been presented as a procedure for moving a complex biosystem toward a set of policy objectives. The manager must formulate strategies that not only achieve these policy objectives, but which retain biological integrity through the political process of adoption and implementation.

Since the origin of wildlife management as a science (Leopold, 1933), research and application have produced an increasing biological background for management decisions. The earliest regulations involved few biological principles beyond protection from hunting, but were accompanied by data collections to monitor certain aspects of regulations. More importantly, the sale of hunting licenses provided funds for the employment of enforcement officers and biologists in wildlife work. The biological groundwork for game management expanded with the establishment of state-federal Cooperative Wildlife Research Units in 1935 and the Pittman-Robertson program in 1937 (Madson and Kozicky, 1971). Today wildlife management is a scientific discipline taught in many colleges and universities. At the same time, the scientific background of other land use disciplines, such as agriculture, forestry, and recreation, has increased dramatically. Along with this increase in scientific know-how, an expanding human population has created greater demands on the finite land base. Thus, wildlife management has become increasingly complex from both economic and scientific viewpoints.

In recent years, biologists have turned to various kinds of analytical models to cope with the increasing complexity of management. A comprehensive review of early modeling work, much of it based on single differential equation analysis, was given by Watt (1968). A more comprehensive analysis for deer management was given by Davis (1967), using dynamic programming, an optimization technique which requires the specification of a single objective. As defined by the California Fish and Game Commission, however, deer management typically involves a multiple objective set, requiring a model to provide information on a diverse set of variables related to the performance of the system. In addition, the model should account for variability beyond the control of management, such as that due to random climatic fluctuations. Computer simulation techniques permitting the development of dynamic models involving random elements have been developed recently (Forrester, 1961), and models of real biological systems have become increasingly common in recent years (Walters and Gross, 1972; Walters and Bunnell, 1971).

Simulation is the mimicking or reproducing of the time behavior of dynamic systems using the digital computer to solve differential and difference equations (Patten, 1971). Simulation of biological systems involves integrating the components of birth and death processes as they relate to such factors as feed conditions, habitat structure, inter- and intraspecific competition, predation, disease, and random fluctuations due to weather. Simulation is a systematic way to integrate a wealth of descriptive knowledge about biological processes which otherwise is available only in fragments. With the computational facility of electronic computers, simulation models can be manipulated with ease to test the effects of various management practices on the biosystem. Without such a model it is often difficult to distinguish the effects of management from other environmental influences. The purpose of the simulation model described in this bulletin is to determine how hunting affects deer numbers and population dynamics.

Objectives of the study were:

1. To develop, test, and refine models simulating existing relationships and values with resources related to deer production and use.

2. To assemble and/or determine the kinds of information needed to clarify the pertinent bioeconomic relationships and values of resources relating to deer production and use.

3. To develop a model encompassing these bioeconomic relationships.

4. To demonstrate the application of the model to deer management and related public policy decision-making.

II. MENDOCINO COUNTY, CALIFORNIA

General Characteristics

Mendocino County includes a diversity of habitat types, some more productive of deer than others. The vegetation types and their acreages are listed in Table 1, together with projected changes by 1980 (California Fish and Game Commission, 1966).

The habitat types that are excellent from the standpoint of carrying capacity for deer make up about 32 percent of the county, including

Table 2. Mendocino County land ownership, 1948[1]

Ownership class	Area in thousands of acres	Percent of county
Public ownership		
Federal		
National forest	174	7.8
Bureau of Indian Affairs	21	0.9
Bureau of Land Management and others	164	7.3
Total federal	359	16.0
State, county, and municipal	102	4.6
	461	20.6
Private ownership	1,785	79.4
Total land	2,246	100.0

[1] Baker and Poli (1951).

coastal forest (particularly after logging), woodland-grass, and hardwood lands. Habitat types intermediate in carrying capacity make up 52 percent of the county and include redwood forest, pine-fir-chaparral, chaparral, woodland-chaparral, riparian, and agricultural lands. The remaining 15 percent of the area inhabited by deer is of lowest carrying capacity, and includes grassland, minor conifers, and coast sagebrush. About 2 percent of the county, namely the urban-industrial areas, lakes, bays, reservoirs, and barren lands, are essentially uninhabitable by deer.

The principal industries in Mendocino County are forestry and agriculture. The next largest industry is tourism and recreation, which includes deer hunting. An important influence on such recreational uses is the land ownership pattern. About 80 percent of the county was privately owned in 1948 (Table 2) and little change in the ownership pattern has occurred since that time. Most of the private land is restricted to hunting by landowners and lessees, resulting in heavy hunting pressure on public lands.

Deer Hunting

The deer hunting season in Mendocino County traditionally is held in August and September. Despite the hot weather at this time of year, hunters seem to prefer hunting before the rutting season (Taber and Dasmann, 1958). The annual bag limit is two bucks, "forked horn or better." With minor exceptions, does, fawns, and spike bucks have not been legal game in Mendocino County since 1901 when bucks-only hunting was introduced as a general statewide policy (Longhurst et al., 1952). The requirement that bucks must have at least one forked antler to be legal game effectively limits hunting to mature animals since nearly all yearling bucks and a sizable fraction of the two-year-old bucks have spike antlers.

There are no systematic records of the number of hunters in Mendocino County. However, a survey (unpublished data, Connolly, 1966) indicated that approximately 16,300 persons hunted deer in the county in 1964. Of this total, 35 percent were residents of the county. In the deer tag returns for 1964, 39 percent of the 4,677 kill report cards for Mendocino County were from county residents. Deer tag sales within the county during 1961-1965 averaged 16,100 per year (Moon, 1972).

From the statewide hunter questionnaire conducted by the California Department of Fish and Game, Macgregor (1972) estimated that there were 25,835 deer hunters in Mendocino County in 1968. Based on these estimates for 1964 and 1968, it seems reasonable that the average number of deer hunters in the county in recent years may have been about 21,000.

One traditional aspect of deer hunting in Mendocino County is the use of dogs, particularly in chaparral or other areas of heavy cover. Data showing the relative efficiency of hunters with and without dogs are quite limited. However, Connolly (1966) found that 11 percent of the deer hunters always used dogs, while an additional 29 percent sometimes used dogs. Sixty percent of the hunters used dogs rarely or never. The hunters who always used dogs claimed a success rate about 70 percent higher than that reported by hunters who never used dogs. It seems questionable whether this difference is solely attributable to the dogs, but the use of dogs is an important element of the sport to many people.

The average deer hunter in Mendocino County, according to Connolly (1966), is male, 39 years old, and has 14 years hunting experience in the county.

Deer Population Data

Virtually the only countywide deer population data available prior to 1958 are the annual hunter tag returns, which provide a minimum estimate of the buck kill annually since 1927. Since 1958, the Fish and Game Department has maintained a unit wildlife manager in this county. With the establishment of this position, herd composition counts and other systematic observations on deer were initiated. This report, therefore, is based largely on data collected during 1958-1970; most of the input and format for the model was developed in 1971. The most useful data for this study were the hunting kill records and herd composition counts.

The reported hunting kill for the years 1958 through 1970 averaged 4,226 bucks annually (Table 3). These include only the bucks for which hunters mailed in the report card attached to each tag, but Fish and Game Department records indicate that the unreported kill may equal at least 50 percent of the reported kill. The estimated age distribution of the buck kill shown in Table 3 may not be representative of the entire county, since these data were collected mainly from public lands where the hunting pressure is greatest. It is generally accepted that the average age of deer killed is inversely related to hunting pressure; i.e. the higher the rate of hunting removal, the lower the average age of deer in the population and, therefore, in the hunting kill. During the 1958-1970 period, the kill averaged less than two deer per square mile of range per year, even if the reported kill of 4,226 is increased to 6,339 to account for unreported kills equal to 50 percent of the reported kill.

Deer herd composition counts are an important part of the Fish and Game Department monitoring program in Mendocino County, as elsewhere in California. These counts are made over standardized routes each year in April and November. The object of the counts is to determine various sex and age ratios in the deer population. During the fall count,

Table 3. Mendocino County buck kill, 1958-1970[1]

Year	Sample size	Percent yearling	Percent 2 year	Percent 3 year	Percent 4+ year	Total reported kill	Kill per square mile
1958	207	1	33	14	52	3,754	1.07
1959	341	0	31	24	45	3,655	1.04
1960	459	5	28	20	47	4,426	1.26
1961	630	1	36	21	42	4,585	1.30
1962	317	1	28	29	42	4,002	1.14
1963	383	2	28	26	44	4,367	1.24
1964	325	2	34	26	38	4,681	1.33
1965	463	1	30	30	39	4,869	1.39
1966	411	1	29	28	42	4,427	1.26
1967	200	2	29	24	45	3,315	0.92
1968	193	6	23	19	52	4,222	1.20
1969	254	3	31	23	43	4,473	1.27
1970	380	2	23	31	44	4,158	1.18
MEAN		2.1	29.5	24.2	44.2	4,226	1.20

[1] California Department of Fish and Game (1971).

animals are classified as spike bucks, legal bucks, does, or fawns to permit calculation of the number of bucks and fawns per 100 does in the population. At this time the fawns are five to six months old. In the following spring, when the fawns are 10 to 11 months old, the deer are classified only as fawns or adults. The Fish and Game Department finds that bucks cannot reliably be separated from does during early spring because the new antlers are quite small at this time of year. In these counts the accent is on herd composition ratios; no attempt is made to count the total numbers of deer.

The average observed spring fawn:adult ratio in Mendocino County during 1958-1970 was approximately 36 fawns per 100 adults (Table 4). Average ratios observed in the fall were 27 bucks and 60 fawns per 100 does. Considerable variation from year to year occurs in the observed fawn:adult ratios. Such variations appear to reflect variable forage conditions due to random deviations in weather from year to year. While the actual fawn losses cannot be calculated directly from herd composition data, these records indicate that the rate of fawn mortality in winter exceeds the rate of adult mortality.

Since 1964, records have been kept of deer killed on state and federal highways in Mendocino County. During 1964-1970, an average of 1,084 dead deer per year was reported by state highway maintenance crews (Table 5). These data include only the animals found dead on the roadway but many more are presumed to leave the pavement before dying.

In addition to hunter kill, herd composition, and highway kill data, the Fish and Game Department maintains a series of deer carcass transects surveyed each spring to obtain relative indices of deer losses each winter. Some fecal pellet count transects are also run annually to determine trends in deer numbers. These data are relatively limited and were not used in this study.

From this review, it is apparent that little is known about the population dynamics of deer in Mendocino County as a whole. However, there is one limited area where a relative wealth of deer population data is available. This is the Hopland Field Station maintained by the University of California in the southeastern part of the county.

An active sheep ranch prior to its acquisition by the university in 1951, the station includes 5,300 acres of oak woodland and chaparral range lands similar to much of north coastal California. A breeding flock which has ranged between 750 and 1,300 ewes has been maintained on the station, and these sheep graze most of the range together with deer. Comparative studies of food habits, reproduction, population dynamics, movements, growth rates, diseases, parasites, nutrition, and physiology of sheep and deer, with supporting range management and range improvement

Table 4. Mendocino County deer herd composition counts, 1958-1970[1]

Year	Spring herd composition: Sample size[2]	Spring herd composition: Fawns/100 adults	Fall herd composition: Sample size[2]	Fall herd composition: Bucks/100 does	Fall herd composition: Fawns/100 does
1958	621	37	791	36	69
1959	972	31	750	37	64
1960	1,284	39	887	33	69
1961	1,104	41	1,093	34	45
1962	708	34	824	29	70
1963	887	45	1,402	23	66
1964	1,173	37	1,571	31	55
1965	1,096	28	1,229	17	41
1966	1,142	18	810	20	46
1967	1,167	27	1,200	19	62
1968	1,018	38	561	25	61
1969	1,175	42	1,656	24	77
1970	1,401	50	1,356	20	52
Mean		35.9		26.8	59.8
Standard deviation		8.4		6.9	11.1

[1] California Department of Fish and Game (1971).
[2] Number of animals classified.

Table 5. Mendocino County highway deer kill, 1964-1970[1]

Year	Classification: Bucks No.	Bucks %	Does No.	Does %	Fawns No.	Fawns %	Unclassified No.	Unclassified %	Total	Kill per mile of checked highway[2]
1964	257	23	590	52	251	22	31	3	1,129	3.2
1965	239	19	673	55	294	24	22	2	1,228	3.5
1966	294	22	718	54	317	24	0	0	1,329	3.7
1967	205	22	426	46	255	27	45	5	931	2.6
1968	242	26	431	45	276	29	0	0	949	2.8
1969	251	23	499	46	303	28	35	3	1,088	3.2
1970	180	19	491	53	224	24	35	4	930	2.7
MEAN	238	22	547	50	274	25	24	3	1,084	3.1

[1] California Department of Fish and Game (1971).
[2] 345 miles of state and federal highways are regularly checked for deer kills in the county. This includes 320 miles of two-lane and 25 miles of four-lane highway.

studies, have constituted a major part of research at Hopland Field Station since its establishment. Deer population data collected routinely since 1951 include herd composition counts, deer hunting and hunting kill statistics, carcass examination data, records of deer collections for scientific purposes, and productivity data. The resident nature of the deer population has been established by observation of live-trapped and marked animals.

Each year since 1954, the Hopland Field Station has been open to controlled public hunting during the regular deer season, in accordance with the same hunting regulations in effect elsewhere in the county. Complete records of the numbers and age composition of bucks taken each year are available.

Deer herd composition data for the Hopland station are more detailed than those from the remainder of the county. At Hopland counts are made annually in April, July, and October. In July and October, the deer are classified as spike bucks, legal bucks, does, or fawns. In April, the deer are tallied as fawns, does, or bucks, since spikes cannot be distinguished from legal bucks when antlers are in an early stage of growth.

Since 1951, all deer carcasses found on the station have been routinely examined to determine the sex, age, date, and cause of death as precisely as possible. A total of 1,282 carcasses was recorded through 1972. These data are particularly useful in establishing mortality patterns and ratios, but do not directly indicate total mortality. However, estimates of relative annual mortality can be made from carcass transect data.

Sick and crippled deer encountered on the field station have been collected for necropsy along with healthy deer as required for various studies, and 1,308 deer were so examined through 1972. Average birth rates for the various age classes of does were determined from fetal counts. The deer population data available from the Hopland Field Station were particularly valuable in the preliminary phases of this study.

Deer Management Problems

The deer of Mendocino County are subject to a variety of pressures and environmental variations, some amenable to control or management. Hunting regulations affect the population and are set by the Fish and Game Commission. However, the effects of hunting, particularly at present harvest levels, have been found to be trivial compared to the forage variations induced by climatic fluctuations from season to season and year to year. These variations interact with forest and agricultural management practices to cause fluctuations in the carrying capacity for deer in various habitat types. On a countywide basis, logging and burning probably have more effect on deer than other human activities. However, the beneficial effects of logging on deer populations are fortuitous and little intentional habitat improvement has occurred except for some of the chaparral burning. Increasing air pollution controls and restrictions on burning permits in recent years have reduced controlled brush burning, while improved fire control techniques (particularly aerial tankers) have significantly reduced the magnitude of wildfire burns.

Biological information indicates that Mendocino County currently supports as large a deer population as the present pattern of land use and habitat structure can maintain. Because the deer ranges are overstocked, the production and survival of fawns are low. Intraspecific competition for limited forage supplies is the primary cause of many kinds of deer problems. The conflicts associated with deer, such as forest and agricultural depredations, deer-auto collisions, and parasite and disease interactions between livestock and deer could be significantly alleviated by reducing deer numbers. Such a reduction could be achieved by an increase in the hunting kill, which would reduce intraspecific competition and thus provide a higher level of nutrition for each animal. This would result in a healthier, more productive deer population.

It is within this framework that the simulation model to provide numerical estimates of deer population responses to various potential hunting practices in Mendocino County was developed. The emphasis in the model is upon the biological characteristics of the relationship between the population size and its habitat. This is a necessary first stage toward modeling some of the broader aspects of management problems.

III. FORMULATION AND VALIDATION OF THE MENDOCINO COUNTY DEER SIMULATION MODEL

The Mendocino County deer population is part of a complex biosystem. The model presented here is an abstract representation of the real biosystem, formulated to bring together its relevant features. It consists of a system of mathematical equations. Their solution gives the status of the system at specified points in time.

The real biosystem includes non-linearities, time-dependent events, negative feedback mechanisms, and stochastic or random components. A mathematical model which includes these complexities is beyond solution by analytical procedures; that is, the system of mathematical equations cannot be solved for all variables for all points in time with the usual simultaneous equations methods. Therefore, a procedure of step-by-step calculations for all variables sequentially through time must be utilized. This procedure—simulation—is most efficiently performed by electronic computers.

Computer Simulation Methodology

Computer simulation methodology has been described (Halter et al., 1970) as a process involving the following steps: (1) problem definition; (2) mathematical modeling and simulation; (3) model refinement and validation; and (4) design and execution of experiments with the model. This methodology was followed in this study. First, the management problem was defined in the context of the policy objectives relating to the deer resource. The problem definition included recognition of the interrelationships within the biosystem, and the links between the biosystem and the political, economic, and social systems.

Next, attempts were made to construct an informal diagrammatic model. Several approaches were taken before the final formulation was selected. Each approach resulted in feedback to problem definition. Changes were made in the approach to the formulation of the model, resulting in compromises between model realism and data availability. Clear definitions of policy objectives for the population, biological relationships, and alternative management strategies were needed. From the diagrammatic model, the mathematical formulation was developed in computer programming format. The model relies upon biological principles as well as available data. Validation procedures included checking the results of the model for consistency with field data and applicable biological principles. The fourth phase of the methodology was the design and execution of experiments with the model.

Components of the Deer Population Simulation Model

The environmental and physiological mechanisms which regulate wild animal populations have been thoroughly discussed in the literature (Allee et al., 1949; McLaren, 1971). In our view, deer numbers in Mendocino County are limited primarily by the nutritional aspects of their environment—quality and quantity of available forage, competition (mostly intraspecific) for forage, and the physical interspersion of food, water, and cover. These relationships are influenced by weather, deer numbers, soil types, and land use patterns. Deer habitat may be viewed as a composite of biotic and physical elements, so that both density-dependent and density-independent relationships exist.

The carrying capacity of deer habitat depends upon weather, soil types, land use practices, and other influences which vary independently of deer density. Of these density-independent factors, weather is probably the most variable from year to year. When deer numbers approach or exceed the carrying capacity, they are regulated by competition for forage and associated density-dependent phenomena. Since deer, through their foraging impacts, can definitely alter the carrying capacity of their range, their effect on the forage supply may be greater than that produced by the weather pattern in a given year.

The principal influences on deer in Mendocino County are related schematically in Figure 1. Deer numbers at any given time are determined by the rates of births, natural losses, and hunting losses. Birth and natural loss rates depend on forage conditions, including habitat structure and competition, which are ultimately set by climatic and physical properties of the habitat. Natural losses also are secondarily affected by predators, parasites, and diseases. The effects of these agents on the deer are mostly density dependent with nutrition as a predisposing factor. In contrast to births and natural losses, hunting losses are density dependent only in the sense that hunting regulations and hunting success are influenced somewhat by deer numbers. Hunting regulations in California are based largely on political and social considerations, and hunting at present accounts for only a small portion of the total mortality.

The regulation of an animal population by variations in births and deaths resulting from nutritional aspects of environmental variations might be cited in the systems science literature as negative feedback (Bertalanffy, 1968). The deer population is not a steady-state equilibrium system, as it is subject to random changes in the weather, food supply, and hunting pressure. The carrying capacity of the deer range is changing continuously, due, for example, to deliberate habitat improvement practices or to natural processes such as successional changes in a forest after logging. Weather variables may interact to give a trend to carrying capacity. The population will then vary around this trend over time due to the negative feedback effects in the system.

In Figure 1 the real flows, causal relationships, and information flows relate to the interactions of the real biosystem. The functional flows indicate those relationships which are utilized in the computer simulation model. Real flows are those which account for the deer numbers, by age and sex, at any time. Thus, given a particular number of deer by age and sex, subsequent births and deaths will result in another population level and another age and sex composition of the population. The population dynamics are generated by time differentials in the birth rates, natural mortality rates, and hunting kill rates (Figure 1). The total of natural losses and hunting kills, which are mutually exclusive, includes all the mortality in both the real biosystem and the simulation model.

The complex of factors in the real biosystem which influence the birth rates and natural mortality rates are shown by the causal linkages. Because these causal relationships could not be quantified directly, due to data limitations, it was necessary to devise proxy variables. The proxy

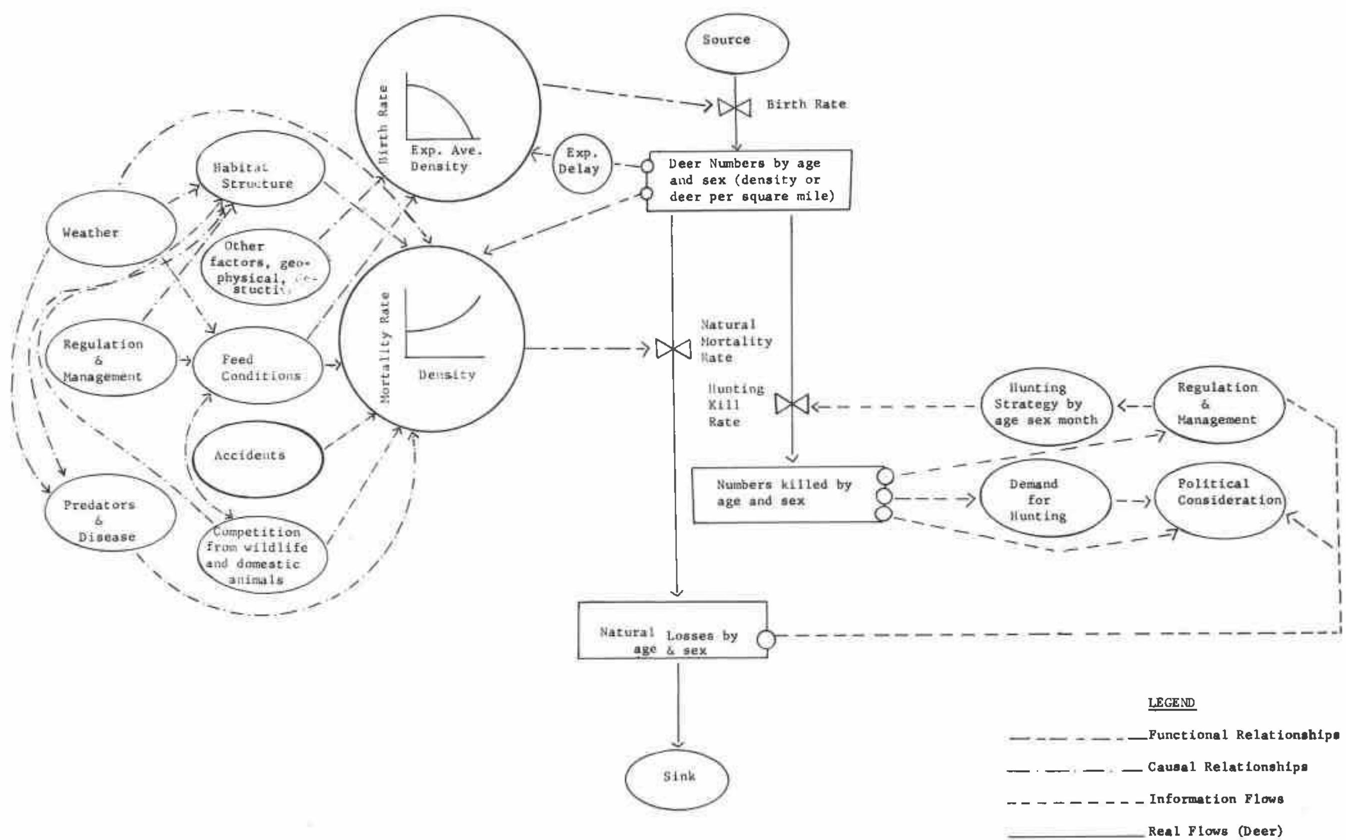

Figure 1. Biomanagement model of the Mendocino County deer population.

variables used in the model are indicated by the functional flows in the figure. In the simulation model, the birth rates and natural mortality rates are generated endogenously, whereas the hunting kill rates are specified exogenously for each run.

In the real world the particular hunting kill rate results from the hunting strategy that is formulated by the state Fish and Game Commission cognizant of political considerations, regulations, management recommendations, and the demand for hunting. Biological performance variables such as the natural losses, total population, and the dimension of the hunting kill in previous years also are inputs into the formulation of hunting strategies. Factors which determine the hunting strategy at any time are connected by information flows as shown in Figure 1.

Natural mortality rates

Natural mortality includes losses due to every cause but hunting—malnutrition, old age, the actions of predators other than man, parasites and diseases, accidents on the highways, and so on.

Since the deer range has a finite carrying capacity, any increase in the size of the population beyond this capacity will further diminish the average plane of nutrition. Natural losses, related directly to the plane of nutrition, decrease as the size of the population falls below the carrying capacity. In addition to the losses due directly to malnutrition, the incidence of parasites increases with deer density and is likewise negatively correlated with nutrition. Effects of diseases and parasites are also accentuated in animals which are malnourished. These factors indicate a clear relationship between density and natural mortality rates. Predators such as the mountain lion, coyote, and bobcat account for an unknown amount of deer mortality in the county, but elsewhere the effects of such predation have been found to be minor compared to nutritional and climatic influences (Hornocker, 1970; Swank, 1958).

Although the relationships of animal populations to so-called density-dependent factors are considered by some to be controversial, we believe the major factors limiting deer density are associated with nutrition. In the model we have used deer density as a proxy variable to express mortality rates as a function of the level of intraspecific competition for forage and related factors. We have not attempted to evaluate the social responses to density but recognize that they exist (Taber and Dasmann, 1958).

Weather (temperature and precipitation) directly influences the natural mortality rates, particularly during the winter months. In addition, weather indirectly influences mortality by its effects on the feed conditions as well as on certain parasites and diseases. The seasonal patterns of weather effects, as reflected mainly in seasonal differences in feed conditions, are made explicit by having natural mortality functions described for each month. A proxy variable called the forage factor has been devised to account for random variability in weather-induced forage variations from year to year.

In the model, density-dependent natural mortality functions are of the general form shown in Figure 2. For each month of the year, natural mortality schedules are defined for the following age and sex groups of deer: fawns, yearling bucks, yearling does, bucks and does two to six years old, and bucks and does seven or more years old. Natural mortality calculations are made each month. At the beginning of the month, the total inventory of deer is computed. This fixes the density (number of deer per square mile). Then, from a natural mortality function for each sex and age class, the mortality rate at the current density is determined and deer numbers in each age class are reduced accordingly.

The mortality functions in the model differ for various age groups of deer because certain age classes are more sensitive than others to intraspecific competition (Longhurst, 1956). Likewise, seasonal changes in sensitivity of the various age and sex classes occur. The different curvatures and positions of the mortality functions for various age and sex classes reflect relative sensitivity to density-dependent factors. For example, the natural mortality functions for fawns for each month are above the comparable functions for middle-aged bucks and does (2-6 years old). Also, the first derivative of the fawn function evaluated at all densities is greater, implying that the increment to mortality for a marginal increase in density is greater among fawns than adults. Determining the relative

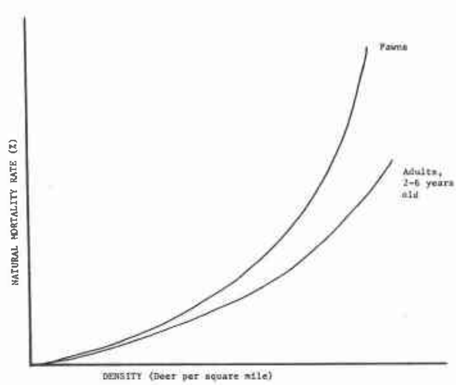

Figure 2. General form of natural mortality functions in the Mendocino County deer simulation model.

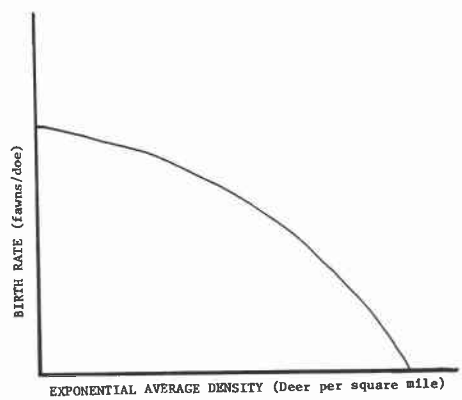

Figure 3. General form of the birth rate function in the Mendocino County deer simulation model.

sensitivity of the various age groupings to natural mortality was an important part of the modeling process.

As presently structured, the model assumes that the carrying capacity of the habitat is constant over time even though it may vary from year to year. However, overstocking (excessive numbers of deer on the range) may, in fact, produce a cumulative long-range downward trend in carrying capacity (Longhurst et al., 1952). Vegetation type projections (Table 1) also indicate that the overall carrying capacity of ranges in Mendocino County for deer may be somewhat lower in 1980 than in 1963, due largely to inundation of habitat by proposed reservoirs and the removal of oak trees from woodland-grass types. However, recent legislation postponing dam construction on the Eel River may alter this projection. Furthermore, it is difficult to forecast levels of future logging or controlled burning, since either could alter the trend in carrying capacity. For these reasons, no long-range projection of carrying capacity changes is included in the model.

Birth rates

In the simulation model, birth rates for does of various ages are related explicitly to a function of deer density in the same sense used for mortality functions. The general form of the birth rate function is given in Figure 3. Whereas the natural mortality rates increase with density, the birth rates are decreasing functions of the exponential average density at the time of ovulation. The exponential average density for each time period is computed as follows:

$$EAD_t = EAD_{t-1} + \frac{1}{T}(D_t - EAD_{t-1})$$

where t = time period (month), D = density (total deer per square mile), EAD = exponential average density (total deer per square mile), and T = exponential smoothing time constant (number of months). The physical conditions of does at the time of ovulation is related to the feed conditions prevailing immediately prior to that time, with greatest weight attached to the most recent time periods. Thus, the exponential average density at the time of ovulation is used as the proxy variable for the array of factors which interact in the real system to determine birth rates.

In the model, four reproductive age groups of does are distinguished: yearlings (at breeding), 2-year-olds, 3- to 6-year-olds, and older. At current deer densities, the birth rates are highest for does aged 3 to 6 years, lower for older does, still lower for 2-year-old does, and lowest for yearling does (Table 11).

For each group of does the biological limit to the reproductive potential is given by the intercept of the function with the vertical axis. The function also intersects the horizontal axis at a density above which no reproduction would be expected because of malnutrition resulting from severe intraspecific competition for forage.

Hunting kill rates

In Mendocino County the hunting mortality includes the reported kill and the unreported kill (deer killed legally but not reported, illegal kill, and wounded deer which escape but die later). In our model these losses are counted collectively as the hunting kill. Hunting losses are specified separately for each age and sex class. Throughout each computer run, the total numbers of deer in each sex and age class at the end of each month are carried forward as the opening inventory for the next month. In months when hunting is desired, the hunting kill for each age and sex class is specified as a fraction of the opening inventory to be removed by hunters during that month. This permits any or all age classes to be hunted at any time of the year at any desired harvest rate. The model permits separate accounting of cripple losses if desired.

The hunting kill rates in the simulation model are specified for every computer run and are not determined endogenously as are the natural mortality and birth rates. Thus, the status of the system in the model does not influence the particular hunting rates once they are specified. This is a simplification of the real world where the status of the system may influence the hunting kill rates, at least in terms of seasons and bag limits. Actual kill rates depend upon numbers of hunters and hunter success rates.

As shown in Figure 1, there is a complex of factors which results in the implementation of a particular set of hunting regulations. These regulations lead to particular hunting kill rates, depending upon hunting pressure and hunter success. In many situations, of course, the kill rates may differ for various age and sex classes of deer. Numerous combinations of regulations, hunting pressure, and hunter success may generate the same total kill, but this model does not relate hunter success or hunting pressure explicitly to the number of deer killed. However, the hunting strategy specifications used in the simulation experiments lend themselves to interpretation in terms of numbers of hunters required and hunting regulations, as shown later.

The forage factor

In the above discussion, the model is presented as deterministic; that is, average forage conditions are assumed in each year. However, the real biosystem is subject to random shocks from variability in weather conditions and other natural phenomena. In the preliminary phases of model development, attempts were made to relate forage production to particular temperature and rainfall conditions. Although information on grassland production was available, the difficulty of collecting reliable data on browse production precluded any reasonable estimation of the relationship. The problem of estimating functions was compounded further by different forage production patterns for each habitat type. An additional difficulty is that forage conditions depend not only on quantity but also on quality. But despite the lack of usable data on forage production, the deer population showed annual variations in birth and death rates which appeared to be related to forage conditions. Such variations are particularly apparent in fawn survival rates (Taber and Dasmann, 1958; Longhurst and Connolly, 1970). Therefore, a proxy variable, the "forage factor," was created to simulate the response of the deer population to natural fluctuations in forage conditions.

The forage factor provides for adjustments in birth and death rates according to forage conditions. Relative to the average year, natural mortality rates are increased in poor forage years and decreased in good years. Birth rates, conversely, are decreased in poor forage years and increased in good years. In our model, five forage factors are defined, corresponding with poor, fair, average, good, or excellent forage conditions. The relative frequency of these forage alternatives is specified in the input, together with the correction values for adjustments of birth and death rates. By specifying that average years will always be selected (that is, forage factor = 3 has a probability of one and other forage factors have a total probability of zero), the simulation model is no longer stochastic; it reduces to a steady-state equilibrium model.

Time Sequence of Events in the Model

Deer in Mendocino County, as elsewhere, exhibit an annual cycle of reproduction synchronous with seasonal forage conditions. The major seasonal events of reproduction, forage conditions, and hunting are shown in Figure 4 (Taber and Dasmann, 1958). In the model this sequence of events is somewhat simplified from the real system. For example, in this county, births occur from April through June, but in the model all the fawns are arbitrarily assigned a June 1 birth date.

In the simulation program, a unit of time must be defined for purposes of calculation. In this model, the one-month interval was selected as the best compromise between adequate representation of population dynamics, data requirements, and computational expense.

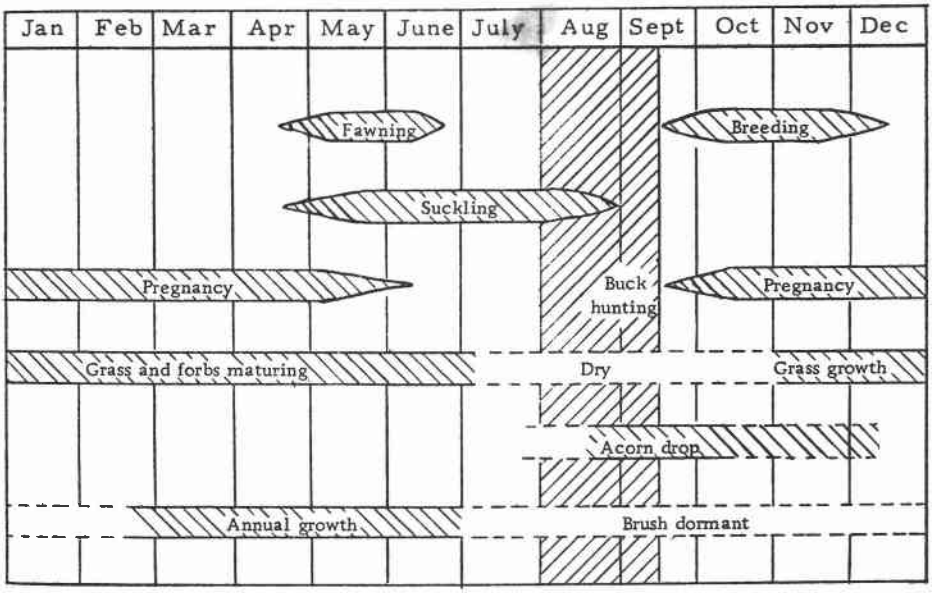

Figure 4. The annual cycle of deer and forage in Mendocino County (modified from Taber and Dasmann, 1958).

Figure 5 shows the main calculations made in each month and each year of a computer run. Each run starts on November 1 and ends on October 31 after completing the specified number of years. In general terms, the program operates as follows: Starting with an opening inventory of deer on November 1, the density and exponential average density are computed and a forage factor is selected as described previously. Natural losses and hunting losses (if any) are computed following the procedures described in previous sections. Loss totals are accumulated by age and sex and the closing inventory for the month is calculated. The closing inventory for the month is the opening inventory for the next month. This basic set of calculations of losses is made each month of the run.

Two accounting years are defined in the computer program. The primary year is from November 1 to October 31. The most detailed herd composition data are taken in November (Table 4), so that the best estimates of deer numbers are made at this time. This accounting year was set to start computer runs when the best estimate of the opening inventory was available. With this primary year, however, accounting problems were anticipated with certain hunting strategies. Buck hunting is traditionally carried out in August and September, while antlerless hunts should most logically occur in November when the animals are in the best physical condition. Therefore, a secondary accounting year, July 1-June

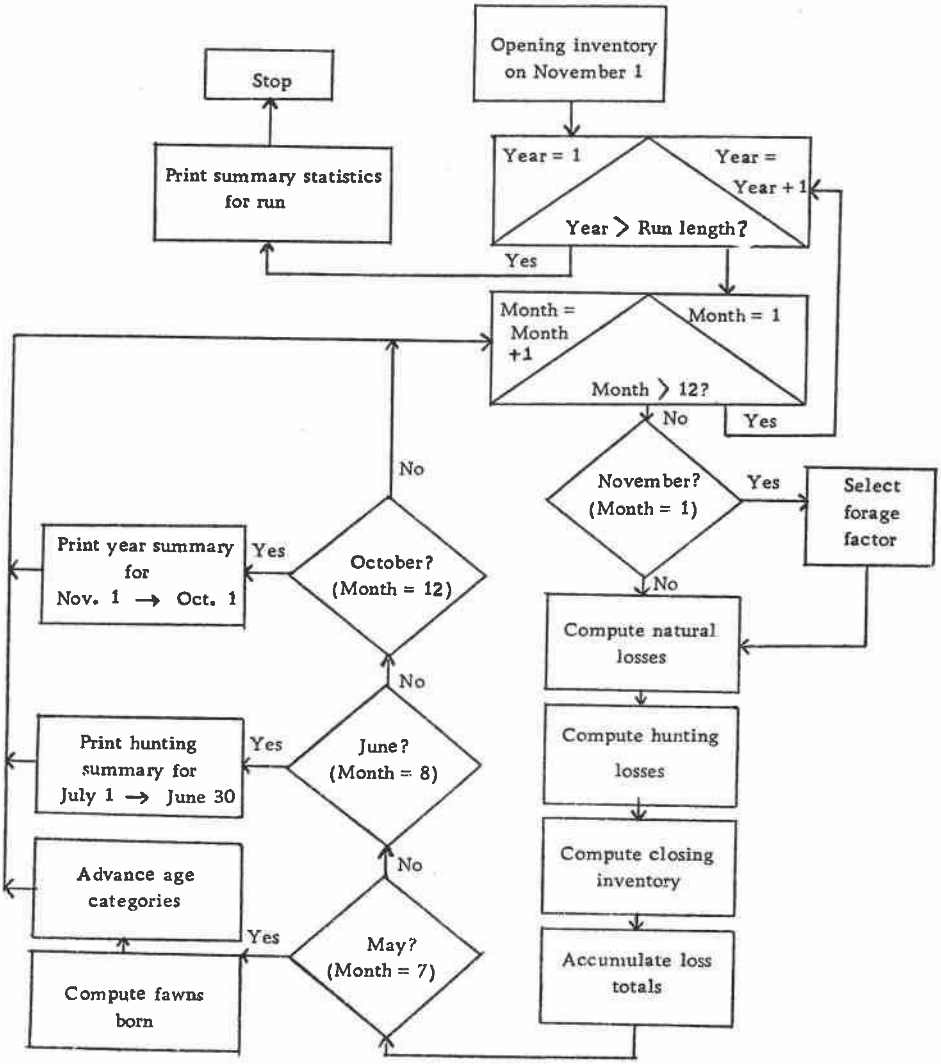

Figure 5. Time sequence of events for the Mendocino County deer population model.

30, was introduced to permit summer buck and fall antlerless hunts to be summarized within the same year. For each accounting year, performance variables are provided by the computer model, including parameters which can be estimated in the field.

In addition to the basic mortality calculations each month and the year-end summaries, a number of special calculations are made in certain months (Figure 5).

November events

The forage factor for each year is generated on November 1 and is applied in all natural mortality and birth rate computations for the next 12 months. The forage factor selected for each year is independent of that selected in any other year. This assumes there is no carryover effect and departs from the real system where successive forage years are not entirely independent. For example, the acorn crop one year may depend upon climatic conditions in the previous year. The model does not include such refinements due to data limitations, but the effect is not considered sufficient to alter our conclusions.

As discussed in the section on birth rates, the exponential average density on November 1 is the proxy variable for the condition of the does at the time of conception. All does are assumed to conceive on November 1. The November 1 exponential average density each year is stored in the computer for application to the does in the population on May 31 the next year to determine the birth rates. This allows for the normal gestation period of seven months.

May events

After accounting for all losses in May and computing the closing inventory, the age categories are advanced (each deer becomes one year older) and the number of fawns born is calculated by multiplying the birth rate for each age category of does by the number of does on May 31. For all age classes of does, the birth rate each year is set according to the exponential average density from the previous November 1.

Fawns are separated by sex at the beginning of their second year (when they become yearlings), according to a sex ratio specified in the input data, and thereafter are accounted for in the other 15 age categories of bucks and does. At the end of their sixteenth year, the remaining bucks and does are dropped from the system. Under a wide range of hunting strategy experiments with the model, the number of deer reaching this age was trivial compared with the total population.

June events

The mortality of fawns in June, the first month after birth, is a function of the exponential average density. This reflects the assumption that the condition of the doe during gestation is the principal factor influencing early fawn mortality (Taber and Dasmann, 1958). If the does are in poor condition, there is high fawn mortality during June, the fawns probably dying in the first hours or, at most, a few days after birth.

The hunting account year ends on June 30. Thus, after accounting for losses in June, the hunting performance variables and other parameters of interest for the last 12 months are summarized.

October events

October 31 completes the main accounting year in the model. After computing the closing inventory for October, the performance of the system for the past 12 months is summarized by a set of selected parameters, several having been monitored at this time each year in the field. When the final year of a simulation run is completed, the means, standard deviations, and coefficients of variation for selected parameters are calculated from the values computed each year of the run.

Input Data

A variety of initial values, parameters, and hunting specifications must be provided as input at the beginning of each run of the model. The first step in the development of these data was to estimate the number of deer in Mendocino County. Average deer numbers were calculated by two methods: ratio estimation and carrying capacity calculations.

Estimation of deer numbers

Ratio estimation method. This approach utilized hunter kill and herd composition data. The legal buck kill during 1958-1970 was estimated to average 6,339 bucks annually, based on the average reported kill of 4,226 (Table 3) plus an allowance of 50 percent for unreported kills. The 50 percent figure for unreported kills is the subjective judgment of biologists familiar with the deer management situation in Mendocino County. The same biologists considered that, on the average, a maximum of 25 percent of the legal bucks were killed by hunters each year. If 6,339 bucks equaled 25 percent of the legal buck population at the beginning of the season, legal buck numbers after the season were 19,017 (3 x 6,339). This figure was taken as the estimated legal buck population on November 1.

On the average, during 1958-1970, about 10 percent of the deer in Mendocino County in November were legal bucks (calculated from Table 9). If 19,000 legal bucks constituted 10 percent of the population, the deer population totaled approximately 190,000 deer, or 55 deer per square mile of habitat.

Carrying capacity calculation. This method involves a summation of separate estimates of deer numbers within each habitat type. Average deer densities estimated by the California Fish and Game Commission (1966) were applied to determine deer numbers within each type. Adding these figures, the total population appeared to contain between 127,000 and 236,000 deer, with 181,000 deer as the most reasonable estimate (Table 6). This agrees closely with the result of the previous method.

Table 6. Deer numbers by habitat type in Mendocino County[1]

Habitat type	Square miles	Deer per sq. mile	Avg. deer per sq. mile	Deer population		
				Minimum	Avg.	Maximum
Redwood	1,042	30–60	45	31,260	46,890	62,520
Coastal forest	530	60–100	80	31,800	42,400	53,000
Grassland	465	10–30	20	4,650	9,300	13,950
Woodland-grass	374	60–100	80	22,440	29,920	37,400
Pine-fir-chaparral	313	30–60	45	9,390	14,085	18,780
Chaparral	255	30–60	45	7,650	11,475	15,300
Hardwood	208	60–100	80	12,480	16,640	20,800
Woodland-chaparral	155	30–60	45	4,650	6,975	9,300
Agriculture	56	30–60	45	1,650	2,520	3,360
Minor conifers	48	10–30	20	480	960	1,440
Coast sagebrush	6	10–30	20	60	120	180
Riparian	.6	30–60	45	18	27	36
Barren	35	----	----	----	----	----
Urban-industrial	15	----	----	----	----	----
Lakes, bays, reservoirs	9	----	----	----	----	----
TOTALS				126,528	181,312	236,066

[1] Longhurst et al., 1969.

Paper and pencil model. The next step in preparation of the input data was a critical review of all available information pertinent to the dynamics of deer in Mendocino County. The most important of these data were described in Section II. It was obvious that existing field data were not suitable for use as input without considerable modification. In particular, it was necessary to construct a paper and pencil model of average deer numbers under existing conditions before the natural mortality schedules could be developed. Because of the relatively detailed information available at the Hopland Field Station, preliminary calculations were made first for deer on the station. Hunting kill, herd composition, trapping, carcass examination, and autopsy records for 1964-1966 were synthesized into a series of seasonal estimates of deer numbers in four sex and age classes (Table 7). These estimates represent the minimum deer population required on the station to support the known legal buck mortality which results almost entirely from hunting. By interpolation and additional calculations, Table 7 was expanded to give estimates for each month of the year for seven age and sex classes of deer: fawns, yearling bucks, yearling does, 2- to 6-year-old bucks and does, and old (7+ years) bucks and does. This expanded model (Table 8) indicates estimated deer numbers on the last day of each month.

Table 7. Average numbers of deer on the Hopland Field Station, 1964-1966[1]

	May	July	October	April
Legal bucks	40	90	50	40
Spike bucks	110	60	50	40
Does	330	320	300	270
Fawns	260	220	200	130
TOTALS	740	690	600	480
Deer per sq. mile	95	88	77	61

[1] Connolly, 1970.

Table 8. Monthly estimates of sex and age classes of deer on the Hopland Field Station (averages for 1964-1966)

Sex and age class	Numbers of deer at end of month											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Fawns	260	225	220	215	210	200	196	186	165	144	134	130
Does												
1	65	64	62	60	57	55	55	54	53	51	50	50
2–6	180	180	180	177	170	163	162	161	157	153	151	150
7+	90	89	87	85	82	80	79	77	73	68	66	65
Bucks												
1	65	64	62	60	54	52	51	49	46	43	41	40
2–6	79	79	79	62	52	52	52	51	50	48	47	47
7+	6	6	6	5	4	3	3	3	3	3	3	3
TOTAL	745	707	696	664	629	605	598	581	547	510	492	485
Deer per sq. mile	95	91	89	85	81	77	77	74	70	65	63	62

Following the development of deer population estimates for the Hopland Field Station, data from Hopland and the remainder of Mendocino County were compared to determine whether the Hopland model was typical of deer in the county as a whole. A number of differences were found between the two areas (Table 9). The Hopland population exhibited greater density, higher fawn survival, lower legal buck to doe ratios, higher spike buck to legal buck ratios, and much higher hunting removals than the county as a whole. The antlerless kill at Hopland results from scientific collections and trapping of deer as required for research purposes. Because of the higher density and hunting removals at Hopland, it was concluded that a separate set of estimates similar to Table 8 would be needed to adequately represent the deer population of Mendocino County.

Table 9. Comparison of deer population data for Hopland Field Station and Mendocino County[1]

Parameter	Average values: Hopland Field Station (1964-1966)	Hopland Field Station (1958-1970)	Mendocino County (1958-1970)
Est. deer numbers (Nov. 1)	600	----	190,000
Deer/square mile (Nov. 1)	77	----	55
Herd composition data			
Fawns/100 adults (May 1)	38	44	36
Fawns/100 does (Nov. 1)	67	74	60
Bucks/100 does (Nov. 1)	33	33	27
Legal bucks/100 does (Nov. 1)	17	16	19
Spike bucks/100 does (Nov. 1)	16	17	8
Hunter kill data[2]			
Annual reported buck kill (deer/square mile of range)	4.3	4.9	1.2
Annual reported antlerless kill (deer/square mile of range)	9.9	6.3	0

[1] From California Department of Fish and Game (1971) and unpublished data on file at the Hopland Field Station.

[2] Excluding cripple loss and unreported kill.

Taking into account the differences between the Hopland and Mendocino County deer populations, a paper and pencil model similar to Table 8 was developed for the county, beginning with the estimate of 190,000 deer on November 1. As this model (Table 10) was to be used for estimating natural mortality rates, the preliminary figures for adult bucks were modified to indicate expected losses in the absence of hunting. For this reason, Table 10 does not account for hunting losses of bucks during August and September.

Due to minor adjustments to achieve consistency of the estimates from each month to the next, the values shown in Table 10 do not agree exactly with herd composition data (Tables 4, 9). However, Table 10 represents the best estimates which could be developed from available data. These figures suggest that on the average during the 1958-1970 years, deer numbers in Mendocino County ranged seasonally between 142,000 and 240,000 animals. With these preliminary calculations completed it was possible to proceed with preparation of input data for the model.

Initial inventory of deer numbers

Table 10 indicates an average of 190,000 deer in Mendocino County at the end of October (November 1). The model requires that the opening

Table 10. Monthly estimates of sex and age classes of deer in Mendocino County (based on data for 1958-1970)

Sex and age class	Numbers of deer at end of month (thousands)											
	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April
Fawns	93.1	63.3	61.4	59.0	56.5	54.2	53.0	49.2	41.6	34.0	30.2	29.0
Does												
1	16.7	16.6	16.5	16.2	15.7	15.0	15.0	14.5	13.7	12.9	12.4	12.3
2–6	43.3	43.2	43.2	42.8	42.2	41.7	41.6	41.2	40.6	40.1	39.9	39.8
7+	46.0	45.4	44.8	44.2	42.9	41.1	40.3	38.5	35.1	31.6	29.8	29.1
Bucks												
1	11.2	11.1	11.0	10.7	10.4	9.9	9.7	9.3	8.4	7.5	7.1	6.9
2–6	22.5	22.5	22.4	22.2	21.9	21.6	21.5	21.3	21.1	20.8	20.7	20.6
7+	7.1	7.1	7.0	6.9	6.7	6.4	6.3	6.0	5.5	4.9	4.6	4.5
TOTAL	240	209	206	202	196	190	187	180	166	152	145	142
Deer per sq. mile	70	61	60	59	57	55	54	52	48	44	42	41

inventory specify deer numbers in each of 31 age and sex classes—fawns, does 1-15 years old, and bucks 1-15 years old. In accordance with Table 10 the opening inventory included 54,000 fawns, 98,000 does, and 38,000 bucks. The does and bucks were apportioned among the age classes 1 through 15 years by graphic methods based upon the relative frequency of each age at Hopland.

During the validation phase, the model was found to be quite insensitive to variations in the size and composition of the opening inventory. Even when a run was initiated with fawns only (no bucks or does), the output indicated the development of a normal population less than 10 years into the run.

Area of occupied deer range

The vegetative types supporting deer in Mendocino County include 2,208,640 acres or 3,451 square miles (Table 6). The latter figure was used in each month of each run to compute the density of deer (number of deer per square mile).

Time constant for exponential average density

This figure is set to indicate the time period prior to ovulation when forage conditions are believed to influence ovulation rates. We have used three months in all runs. In the model, ovulation occurs on November 1. By relating ovulation rates to the exponential average density (EAD) over the previous three months, the ovulation rates are influenced most by density (forage conditions) in October with carryover effects from September and August.

In the model, fawn mortality during June, the first month after birth, is also a function of EAD. This reflects our conviction that the condition of the doe during late gestation is the principal influence on early fawn mortality. The EAD was conceived as an expression of cumulative nutritional effects over time periods longer than the basic calculation interval (one month). In practice with the model, however, the EAD agrees closely with deer density at any given time.

Proportion of 12-month-old male fawns

On June 1 in each year of a run, this proportion is used to separate the 12-month-old fawns into yearling bucks and does. This value was set initially at 0.5 and subsequently adjusted as discussed later in connection with model validation.

Proportion of legal bucks in second and third years

These values are needed to simulate selective hunting of "forked-horn or better" males, as specified in current California hunting regulations. Firm estimates are not available, but in all runs we have assumed that 10 percent of the yearlings and two-thirds of the 2-year-old bucks have legal antlers. There is evidence that these values not only vary annually with forage conditions, but also differ among various regions within the county. However, existing data were insufficient to permit these sources of variation to be incorporated into the model.

Natural mortality schedules

The natural mortality schedules are used to estimate the fraction of the deer that die of natural causes during each month. Separate schedules for each sex and age class of deer for each month were derived graphically from Table 10. For each age group in each month, the difference between estimated deer numbers at the beginning and the end of the month was expressed as a fraction of deer numbers at the beginning of the month. This fraction was then plotted against the estimated deer density at the beginning of the month. A smooth curve was drawn from the origin of the graph through the plotted point, giving an increasing rate of mortality as density increased (Figure 2). Mortality values were read from the graph at intervals of 10 deer per square mile to give a schedule for densities from 10 to 160 deer per square mile.

For example, the number of fawns in Mendocino County was estimated to decline 1,200 during November (Table 10), a loss of 0.022. A curve drawn from the origin through the value of 0.022 at a density of 55 deer per square mile (Figure 2) provided the natural mortality schedule for fawns for November. The curves for other months and other age classes were derived similarly, except for fawns in their first month of life (June). The fawn mortality schedule for June is a function of the EAD on June 1, as explained previously.

While the model in its present format involves deer in 31 sex and age classes, we have used only five sets of mortality functions: one each for fawns, yearling bucks, yearling does, deer 2-6 years old, and deer 7+ years old.

Birth rate schedules

As noted earlier, birth rates in the model are calculated separately for four age groups of does. These age classes are identified in Table 11, together with average birth rates determined by fetal counts at the Hopland Field Station. Estimates of productivity elsewhere in the county were not available. Extreme high and low productivity values observed in good and bad forage years, respectively, are also shown for each age class. For each class of does, the average pregnancy rate was plotted against the average deer density in the county November 1, and the expected productivity at higher and lower densities was estimated graphically (Figure 3). The functions for young does exhibit greater sensitivity to changes in density than those for middle-aged and older does, consistent with available information.

Forage factor specifications

Input data required to operate the forage factor (FF) include an initial random number, the probability distribution of forage years (five alternatives), and five sets of correction values applied to births and natural losses.

Table 11. Pregnancy rates in deer at the Hopland Field Station, 1951-1969

Age of doe[1]	Does examined	Fetuses examined	Percent pregnant	Pregnancy rates (fetuses/100 does)	
				Average	Extremes
1 year	36	15	36	42	1-100
2 years	35	36	91	103	50-135
3–6 years	132	195	98	148	100-180
7+ years	90	127	93	141	90-170

[1] At breeding. Each doe becomes one year older at parturition.

Table 12. Calculation of probability distribution of forage factors from Mendocino County herd composition data, 1958-1970

Fawns/100 adults (spring)[1]	Fawn survival	Number of years observed[1]	Relative frequency	Forage factor
18-26	Poor	1	0.0769	1
27-32	Fair	3	0.2308	2
33-38	Average	4	0.3077	3
39-44	Good	3	0.2308	4
45-50	Excellent	2	0.1538	5
Totals		13 years	1.0000	

[1] From Table 4.

The probability distribution of poor, fair, average, good, and excellent forage years was calculated from herd composition data (Table 12). The fawn:adult ratios observed each spring for 13 years were arbitrarily grouped into five fawn survival classes ranging from poor to excellent. The relative frequency of the observed fawn survival classes was then taken as the probability distribution of poor, fair, average, good, and excellent forage years. The model permits the probability distribution of forage factors to be changed as an experimental variable and is quite sensitive to changes in this distribution.

The basic principle of the mortality corrections is that, relative to the average year, natural losses are increased in poor forage years and decreased in good years. The correction coefficients for fawns were calculated from estimates of the average fawn:adult ratios at birth and the variable fawn:adult ratios recorded each spring in herd composition counts (Table 13). The midpoints of the fawn survival classes from Table 12 were subtracted from the average estimated fawn:adult ratio at birth to obtain an estimate of relative fawn losses in poor, fair, average, good, and excellent years. From these values, the fawn losses for each survival class were expressed as a fraction of losses in average years (FF = 3). These fractions were used as the FF corrections for fawn mortality.

The mortality correction factors for yearlings and older deer were intended to indicate, relative to fawns, the sensitivities of these age classes to forage variations. The correction coefficients (Table 13) were set arbitrarily to give half as much variability among yearlings and old deer as among fawns, and one-fourth as much variability for middle-aged deer as for fawns. This reflects the knowledge that certain age classes of deer are more vulnerable to adverse conditions than others (Longhurst, 1956). Similarly, the effects of good forage are more apparent in some age classes than others. While the resulting values for mortality adjustments (Table 13) are subject to question, we believe that the principles are correct.

Table 13. Calculation of natural mortality correction coefficients for the Mendocino County deer population

Forage factors	1	2	3	4	5
Observed fawn survival[1] (fawns/100 adults in spring)	18–26	27–32	33–38	39–44	45–50
Midpoint of fawn survival class (fawns/100 adults)	22	29	35	41	47
Average birth rate[2] (fawns/100 adults)	63	63	63	63	63
Fawns lost during first year (fawns/100 adults)	41	34	28	22	16
Fawn losses relative to average year	41/28	34/28	28/28	22/28	16/28
Corrections to average natural mortality					
Fawns	1.46	1.21	1.00	0.79	0.57
Bucks and does					
Yearlings	1.23	1.11	1.00	0.90	0.78
2-6 years	1.12	1.05	1.00	0.95	0.89
7+ years	1.23	1.11	1.00	0.90	0.78

[1] From Table 12.
[2] Calculated from data of Table 10.

Modifications of these mortality coefficients during model validation are discussed later.

For each of the five FF alternatives, birth rate corrections are needed for four age classes of does. As indicated in Table 11, pregnancy rates in deer are variable with forage conditions. Such variations seem to be greatest among yearling does, less for 2-year-old and old (7+ years) does, and least for middle-aged does. The natality corrections associated with forage factors in the model were derived from pregnancy data for the various age classes of does under differing forage conditions (Table 14). The natality correction coefficients for forage factors 1 and 5 represent the extreme values from Table 11 expressed as fractions of the average values within each class of does. The coefficients for forage factors 2 and 4 were then established by interpolation. While the resulting set of correction coefficients is somewhat arbitrary, we feel that the general relationships expressed are correct.

Modification of the FF correction values for natality is discussed later, in connection with model validation.

Table 14. Natality correction values for the Mendocino County deer population model

Age of doe[1] (years)	Forage factors				
	1	2	3	4	5
1	0.02[2]	0.60	1.00	1.30	2.38
2	0.49	0.80	1.00	1.15	1.31
3–6	0.67	0.90	1.00	1.10	1.20
7+	0.64	0.85	1.00	1.10	1.20

[1] At breeding.
[2] .02 = 1/42.

Hunting strategy specifications

The model permits hunting removals in any month from any of 31 sex and age classes—fawns, bucks 1-15 years old, and does 1-15 years old. For each class to be hunted in each month hunting is to occur, the fraction of the opening inventory to be taken by hunters during that month is specified. Zeros are entered for each month for each age and sex class when no hunting is desired.

The existing hunting strategy in Mendocino County results in an estimated 25 percent of the legal bucks being killed annually, with no hunting of does, fawns, or spike bucks. The hunting season opens early in August and closes in late September, and about two-thirds of the total buck kill is taken in August. The hunting specifications developed to simulate this hunting strategy (Table 15) were first devised to account only for the hunting kill of legal bucks (including unreported kills), and later were

Table 15. Hunting specifications to simulate the current hunting strategy in Mendocino County (25% legal buck kill)

	Hunting removals[1]			
	Original		Revised[2]	
	August	September	August	September
Fawns	0	0	0.0003	0.0002
Does 1-15 years old	0	0	0.0013	0.0007
Bucks 3-15 years old	0.167	0.083	0.1670	0.0830
Bucks 2 years old	0.121	0.046	0.1236	0.0619
Yearling bucks	0.017	0.008	0.0210	0.0105

[1] Values shown are fractions of the total number of deer in the class at the beginning of the month taken by hunters during the month.
[2] Includes cripples and illegal kills.

revised to include a minimal illegal kill of spike bucks, does, and fawns. The hunt specifications for yearlings and 2-year-old bucks differ from those for older bucks because only a fraction of the young bucks grow legal antlers.

In all runs of the model cripple losses have been included in the hunting specifications (Table 15). However, the model permits cripple losses to be calculated separately from other hunting losses if desired. This requires a separate set of cripple loss specifications as input, in addition to the hunting rates described above.

Output Specifications and Format

Any endogenous variable from a simulation run can be provided as output of the model. Because routine use of the model can involve large numbers of runs, the input data are printed as part of the output. In addition, the results of each run are summarized in four sections as follows:

1. November 1-October 31 accounting year summary. For each year of the run the following values are printed:

- The forage factor operative for the year
- The deer density and total number of deer at year end
- Total natural and hunting losses during the year
- Ratios of legal bucks, spike bucks, and fawns to does at year end
- Ratio of fawns to does in the previous spring
- Average birth rate in the previous spring
- Average ages of bucks and does at year end.

2. July 1-June 30 hunting year summary. For each year of the run the following values are printed:

- Numbers of legal bucks, spike bucks, does, and fawns on July 1
- Total deer numbers on July 1
- Numbers of legal bucks, spike bucks, does, and fawns taken by hunters during the previous 12 months
- Total number of deer taken by hunters during the previous 12 months
- Total hunting kill during the previous 12 months as a fraction of total deer numbers on July 1.

3. Details of deer numbers, births, and losses during the last account-year of the run. For each of the last 12 months of a run, natural and hunting losses are given along with the inventory of deer in each age and sex class. The number of fawns born is also shown. These data permit detailed examination of the calculations after the model has responded to the hunting strategy under consideration.

4. Statistical summary. The performance of the model throughout the run is characterized by a display of the means, standard deviations, and coefficients of variation of selected parameters:

- Total number of deer on November 1
- Total number of deer on July 1
- Total numbers of legal bucks, spike bucks, does, and fawns on July 1

- Annual natural losses
- Annual hunting losses
- Annual hunting losses of legal bucks, spike bucks, does, and fawns
- Ratio of fawns to does each spring
- Ratios of spike bucks and fawns to does each fall.

The output parameters from different runs can be compared to determine the relative merits of various hunting strategies. Prior to these comparisons the output summaries were used to validate the model.

Model Validation

For a simulation model to be valid, results from the output must be: (1) consistent with all applicable biological principles, and (2) in agreement with available field data indicating the status of the biosystem.

Following is a list of general validation criteria based on biological principles:

1. Total deer numbers must not increase beyond reasonable limits, as defined by the carrying capacity.

2. There is a limit to the amount of hunting that can be sustained by the population. When this limit is exceeded, the population tends toward zero.

3. Buck to doe ratios increase or decrease respectively with decreases or increases in the intensity of selective buck hunting.

4. Fawn to doe ratios increase as the intensity of doe hunting increases.

5. The average ages of the components of the population being hunted decrease as increasing percentages of those components are taken by hunting.

6. The birth rate per doe increases as the population is reduced below carrying capacity by increased hunting removals.

In the validation process, agreement of the output with available field data was achieved through repeated revision of input data, experimentation on the computer, and checking for consistency, until a satisfactory correlation was reached. The acceptable degree of correlation was a matter of judgment of the investigators.

To illustrate the validation process, selected results from three 30-year runs are compared with field data in Appendix A. These runs illustrate the improved agreement between computer output and field data resulting from corrections and revisions in the input.

IV. TESTS OF ALTERNATIVE HUNTING STRATEGIES

Although hunting is only a part of wildlife management, regulation of hunting pressure is often the only management tool available. The tangible values of deer to society also depend largely on the amount of hunting permitted, so hunting regulations directly affect the net value of the deer resource. For these reasons, our experiments with the model have been directed toward the hunting aspect of management.

In the design of hunting strategies, the options of game managers are limited because certain strategies that are biologically feasible may be socially or politically unacceptable, or, alternatively, those which are socially or politically desirable may be biologically undesirable. For example, heavy selective fawn hunting would be an effective means of maximizing the annual hunting kill, but the strategy has never been seriously considered because fawn hunting is not likely to be popular with hunters. The difficulty of distinguishing among deer of certain sex and age classes in the field further limits the practical range of hunting options.

Eight simulation runs with different hunting strategies were tested in the model. This array includes the range of options which could be practically implemented in Mendocino County. The results are presented in tabular form with portions of the output summarized graphically as well. These results describe the impact of selected hunting strategies on population dynamics. Actually, these so-called strategies are rates of removal or kill and do not include hunter success relationships.

Each of the eight strategies described in this section was tested first with the stochastic element of the model (forage variations) suppressed. Such runs are considered "deterministic" because in the absence of forage variations a stable solution is achieved, usually within the first 10 to 15 years of the run. These deterministic runs (Table 16) were then repeated with the stochastic element (forage factors) functional; that is, with random year-to-year variations in forage conditions. The stochastic runs are summarized in Table 17. In each case the final inventory of deer from the deterministic run was used as the opening inventory for the stochastic run with the same hunting strategy. By starting each run with the corresponding deterministic solution values, the transient effect of prior hunting strategies was effectively removed.

In all eight simulation runs, buck hunting, when specified, was conducted in August and September in accordance with the existing custom. Approximately two-thirds of the bucks were taken in August and the remainder in September, simulating the distribution of the kill under current regulations. Antlerless hunts, when specified, occurred in November, the most logical time in view of the relatively good conditions of does

Table 16. Final population and hunting statistics from 30-year deterministic runs of the Mendocino County deer population model[1]

Parameter	Run 1	Run 2	Run 3	Run 4	Run 5	Run 6	Run 7	Run 8
Hunting specifications[2]								
Legal bucks	0	25	50	0	25	50	25	50
Spike bucks	0	0	0	0	0	50	5	5
Does	0	0	0	25	25	15	15	15
Fawns	0	0	0	0	0	80	5	5
Total deer November 1	193,715	192,977	193,145	147,144	148,283	28,043	171,761	172,619
Annual natural losses	94,092	101,043	104,835	28,094	31,046	1,037	54,201	57,183
Annual hunting kill	0	6,327	8,146	11,461	25,208	15,461	23,533	27,118
Legal buck kill	0	5,878	7,612	0	8,734	625	7,526	9,727
Natural/hunting losses	--	16.0	12.9	2.4	1.2	0.07	2.3	2.1
Hunting kill/total deer July 1	0	.03	.04	.08	.15	.52	.12	.14
Natural losses/total deer July 1	.45	.47	.48	.18	.19	.03	.29	.30
Composition of hunting kill (%)								
Legal bucks	0	93.0	93.4	0	34.6	4.0	32.0	35.9
Spike bucks	0	3.1	3.3	0	1.0	3.8	3.6	3.3
Does	0	3.4	2.8	100	64.3	10.9	53.4	50.4
Fawns	0	0.5	0.4	0	0.1	81.3	11.0	10.4
Birth rate (fawns/doe)	1.19	1.18	1.18	1.24	1.23	1.71	1.19	1.19
Total fawns born	94,360	107,568	113,187	40,534	56,316	16,192	77,840	84,400
Fawn survival to 12 months of age (%)	30	30	30	60	60	19	45	45
Herd composition ratios								
Legal bucks/doe (November 1)	.45	.18	.09	1.33	.44	.07	.29	.14
Spike bucks/doe (November 1)	.12	.12	.11	.23	.22	.07	.17	.16
Fawns/doe (November 1)	.56	.56	.56	.65	.65	1.40	.62	.62
Fawns/doe (May 1)	.36	.37	.37	.74	.75	.32	.55	.55
Average age November 1 (years)								
Bucks	4.76	3.12	2.29	6.10	3.59	2.59	3.37	2.38
Does	4.86	4.84	4.83	3.50	3.49	5.51	4.08	4.08

[1] Runs 1 and 7 were 20-year runs; run 2 was a 25-year run; run 6 was a 55-year run.
[2] Percentages of each component taken by hunting each year.

Table 17. Average population and hunting statistics from stochastic 30-year runs of the Mendocino County deer population model

Parameter	Run 1	Run 2	Run 3	Run 4	Run 5	Run 6	Run 6A	Run 7	Run 8
Hunting specifications[1]									
Legal bucks	0	25	50	0	25	50	50	25	50
Spike bucks	0	0	0	0	0	50	50	5	5
Does	0	0	0	25	25	15	15	15	15
Fawns	0	0	0	0	0	80	60	5	5
Total deer November 1	191,750	195,204	197,921	151,461	150,965	22,044	134,535	169,248	170,198
Annual natural losses	94,092	99,621	104,777	28,728	32,771	782	17,840	51,596	53,802
Annual hunting kill	0	6,373	8,362	11,735	25,592	12,041	54,078	23,186	27,286
Natural/hunting losses	--	15.6	12.5	2.4	1.3	.06	.33	2.2	2.0
Hunting kill/total deer July 1	0	.03	.04	.08	.15	.52	.37	.12	.14
Natural losses/total deer July 1	.46	.46	.47	.18	.20	.03	.12	.28	.28
Birth rate (fawns/doe)	1.16	1.17	1.18	1.26	1.20	1.69	1.32	1.16	1.17
Herd composition ratios									
Legal bucks/doe (Nov. 1)	.48	.18	.09	1.32	.42	.07	.08	.29	.15
Spike bucks/doe (Nov. 1)	.13	.12	.11	.23	.21	.06	.07	.17	.16
Fawns/doe (Nov. 1)	.57	.57	.58	.67	.64	1.38	.93	.62	.62
Fawns/doe (May 1)	.36	.37	.37	.75	.75	.32	.40	.54	.55
Average age Nov. 1 (years)									
Bucks	4.91	3.10	2.28	6.08	3.47	2.60	2.65	3.37	2.47
Does	4.80	4.83	4.80	3.49	3.57	5.51	4.79	4.11	4.01

[1] Percentages of each component taken by hunting each year.

in late fall. For convenience, and in the absence of evidence to the contrary, the hunting removal of legal bucks and does was taken as a constant percentage of all age classes. The hunting specifications included an allowance for unreported kills.

Throughout the following discussion deer numbers are shown to the nearest animal. This implies an unrealistic level of precision, but was necessary to permit comparison of various statistics calculated from the output.

Results with Deterministic Assumptions

The following hunting strategies were tested in the simulation runs of the model:

Run 1: no hunting
Run 2: 25 percent legal buck kill
Run 3: 50 percent legal buck kill
Run 4: 25 percent doe kill
Run 5: 25 percent legal buck and 25 percent doe kill
Run 6: 50 percent buck, 15 percent doe, and 80 percent fawn kill
Run 7: 25 percent legal buck, 15 percent doe, 5 percent spike, and 5 percent fawn kill
Run 8: 50 percent legal buck, 15 percent doe, 5 percent spike, and 5 percent fawn kill.

Run 1

Run 1 (no hunting) simulated complete protection from hunters. The total November 1 population was 193,715, and 94,092 deer died of natural causes each year (Table 16). Annual natural losses equaled 45 percent of the total July 1 population. The birth rate was 1.19 fawns per doe and 30 percent of the fawns born reached one year of age. The November 1 population included 0.45 legal bucks, 0.12 spike bucks, and 0.56 fawns per doe. Differential winter losses resulted in a spring (May 1) ratio of 0.36 fawns per doe. The average ages of bucks and does on November 1 were 4.76 and 4.86 years, respectively.

Run 2

This run (25% legal buck kill) simulates hunting as practiced in Mendocino County during the past 20 or more years. From run 1 to run 2 the total population was reduced very little, from 193,715 to 192,977. However, natural losses increased from 94,092 to 101,043. The birth and fawn survival rates remained approximately the same as in run 1.

In run 2, 93 percent of the 6,327 deer taken were legal bucks (Table 16); the remainder were illegal kills of spike bucks, does, and fawns. Hunting and natural losses, respectively, account for 3 percent and 47 percent of the July 1 population; 16 deer died of natural causes for each deer taken by hunters. In response to selective hunting, the legal buck to doe ratio decreased to .18 but other herd composition ratios did not change from run 1. The average age of bucks also declined to 3.12 years, while the average age of does did not change from run 1.

Run 3

This run (50% legal buck kill) represented an apparent doubling of the hunting removal from run 2, with hunting limited to legal bucks only. The total November 1 population did not differ significantly from runs 1 and 2. However, the total natural losses of 104,835 in run 3 represented a further increase from run 2 over run 1. Birth and fawn survival rates were unchanged from the first two.

The hunting kill in run 3 totaled 8,146 deer per year, including 7,612 legal bucks, and amounted to 4 percent of the total July 1 population. In contrast, annual natural losses equaled 48 percent of the July 1 population. The ratio of natural to hunting losses declined somewhat from run 2, to about 13:1. The ratio of legal bucks to does declined to 0.09 legal bucks per doe, while other herd composition ratios were essentially unchanged from runs 1 and 2. The average age of bucks also showed a further decline from run 2 to 2.29 years. The average age of does remained unchanged.

Impact of buck hunting on population dynamics. The percentage of bucks taken by hunting in run 1, run 2, and run 3 represent three points on a continuous scale of possible buck harvest rates with other parameters held constant for the three runs. Hence the response of the system to any practical level of legal buck harvest can be evaluated. Figure 6 shows the total November 1 population, natural losses, and the hunting kill as func-

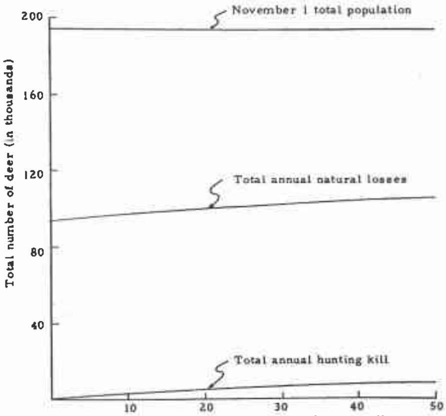

Figure 6. November 1 population, natural losses, and hunting kill as functions of the percentage of legal bucks removed annually by hunters.

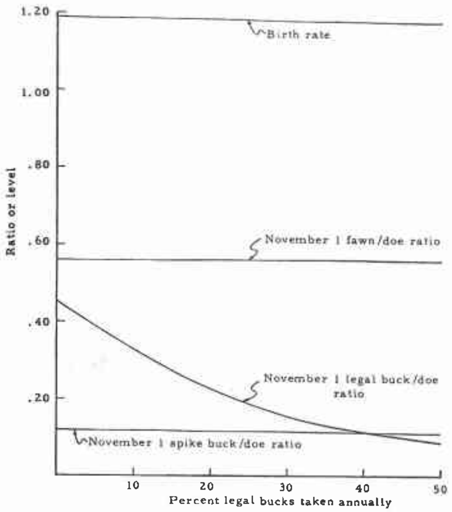

Figure 7. Birth rate and fall herd composition ratios as functions of the percentage of legal bucks taken annually by hunters.

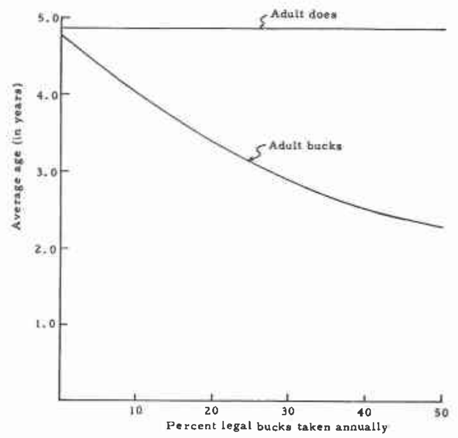

Figure 8. Average age of adult bucks and does as functions of the percentage of legal bucks removed annually.

tions of the percentage of legal bucks taken. In Figure 7, the dependent variables presented are the average birth rate and the legal buck, spike buck, and fawn to doe ratio on November 1. Figure 8 shows the average ages of bucks and does as affected by the percentage of the legal bucks taken by hunting. Figure 6 indicates that selective buck removals at any level between zero and 50 percent annually do not alter total deer numbers, although natural losses increase somewhat with the intensity of buck hunting. Figures 7 and 8 show that the impact on herd performance of the legal bucks-only hunting is restricted primarily to the buck component of the population. The reproductive performance of the individual does does not change, but the number of does increases as buck numbers are reduced by progressively heavier hunting removals. As doe numbers increase, the number of fawns born each year also increases. Since the number of deer dying equals the number born in the long run, the number of deer dying each year also increases with the intensity of selective buck hunting. This is the reason for the increased natural mortality associated with increasing intensity of buck hunting (runs 1, 2, and 3 in Table 16). (In the model the carrying capacity of the habitat was constant for all runs, and deer numbers were apparently limited by the carrying capacity at all levels of bucks-only hunting). As indicated in Figure 7, the average age of does is not influenced by selective buck hunting, but the average age of bucks declines as hunting increases.

There seems to be a practical limit to the vulnerability of bucks to hunters. At the Hopland Field Station with good access and heavy hunting pressure, an estimated 40 to 45 percent of the legal bucks is removed by hunters each year. Elsewhere in Mendocino County hunting access is restricted by poor road distribution, heavy vegetative cover, and private land closures. The vulnerability of bucks to hunters could be increased by setting the hunting season later to coincide with the rut (breeding season) or by lengthening the season and increasing the bag limit. However, the model showed that in the long run the legal buck kill increased only 29 percent from run 2 to run 3 (Table 16) even though the hunting removal was raised from 25 to 50 percent of the legal bucks annually. This increase was achieved at the expense of trophy quality—the average age of bucks decreased almost one year from run 2 to run 3. Given the limitations on hunting access and the likelihood of diminishing hunting pressure as the density of legal bucks declines, it seems doubtful that more than 50 percent of the legal bucks in the county could be taken annually by sport hunting. Thus, run 3 probably indicates the maximum potential kill possible in the county with bucks-only hunting.

Selective buck hunting appears to be a self-limiting phenomenon. Increases in the intensity of buck hunting may produce higher hunting kills for a few years, but in the long run will tend to reduce the number of adult bucks in the population. Regardless of the intensity of hunting, the kill is ultimately restricted to a small fraction of the potential productivity of the population.

Run 4

This strategy (25% doe kill) was run to test the population control produced by selective doe hunting compared with selective buck hunting. Compared with run 1, the total November 1 population was reduced by 24 percent and the total natural losses by 70 percent. Despite the reduction in total deer numbers, the annual hunting kill of 11,461 was greater than that achieved with selective buck hunting even at the 50 percent level. The ratio of natural to hunting losses dropped abruptly to 2.4 to 1. Total mortality equaled only 26 percent of the total July 1 population, compared with 50 to 52 percent in the selective buck hunting strategies. In run 4 the numbers of breeding does and of fawns born were reduced and the birth and fawn survival rates were increased, compared with runs 1, 2, and 3.

As a result of selective doe hunting in run 4, the ratios of legal bucks, spike bucks, and fawns to does in the population all increased, relative to no hunting (run 1) or selective buck hunting (runs 2 and 3). The average age of bucks increased to 6.1 years while that of the does decreased to 3.5 years.

Impact of doe hunting on population dynamics. Comparison of run 4 with runs 2 and 3 demonstrates significant differences in impact on population dynamics of selective doe and buck hunting. The impact of doe hunting on selective parameters is summarized in Figures 9, 10, and 11. These figures correspond to Figures 6, 7, and 8 respectively, permitting a direct comparison of does-only versus legal bucks-only hunting.

This comparison shows that selective removals of bucks at any practicable harvest rate have little effect on deer numbers, whereas the hunting of does even at relatively low levels has a marked effect. Thus, if a reduction of deer density is required to alleviate agricultural or forest depredations, selective buck hunting will not be successful. Similarly, if the objective of management is to maintain a high buck to doe ratio to maximize aesthetic values, selective buck hunting is not the proper approach. If hunters are interested only in the number of deer bagged, the doe-hunting strategy provides a greater kill. However, trophy values are an important part of deer hunting, and doe hunting would not satisfy this

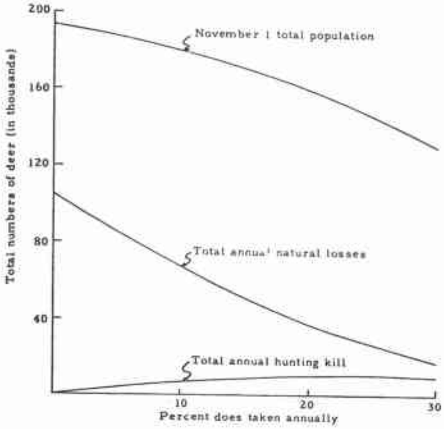

Figure 9. November 1 population, natural losses, and hunting kill as functions of the percentage of does removed annually.

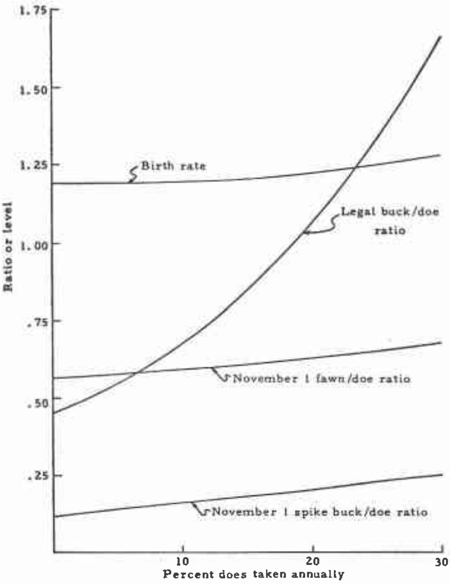

Figure 10. Birth rate and fall herd composition ratios as functions of the percentage of does removed annually.

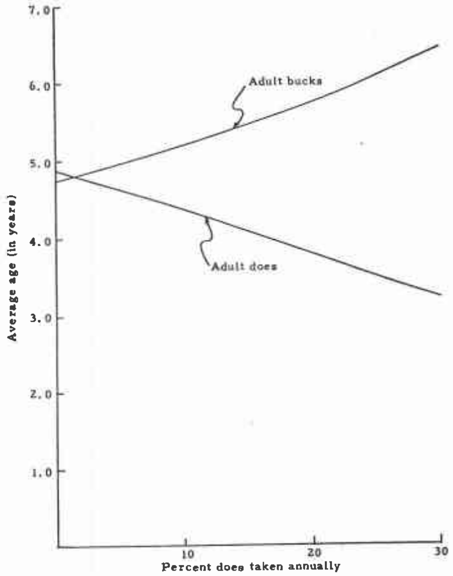

Figure 11. Average age of adult bucks and does as functions of the percentage of does removed annually.

objective. These considerations lead to the examination of a combination of buck and doe hunting.

Run 5

This strategy (25% legal buck and 25% doe kill) was a composite of runs 2 and 4. Comparing run 5 with run 4, the hunting of legal bucks in addition to does increased the hunting kill, the November 1 population, and the total natural losses. The number of legal bucks taken in run 5 was 8,734, 49 percent higher than under the 25 percent legal bucks-only strategy (run 2). In run 5, the legal buck to doe ratio of 44 to 100 was of the same order of magnitude as in run 1 under no hunting. The total natural losses increased from run 4 to run 5, paralleling the increase from run 1 to run 2. Birth and fawn survival rates in run 5 were similar to those in run 4.

As expected, in run 5 the average age of bucks was much lower than in run 4. Because the density was lower in run 5 than in run 2, as indicated by the lower total November 1 population, natural losses of bucks surviving hunting were lower and hence the average age of bucks was higher in run 5 than in run 2. In run 5 about 12 deer died of natural causes for every 10 taken by hunting, giving the lowest natural loss to hunting kill ratio of any strategy considered so far.

Run 6

In this run, 50 percent of all bucks (both legal bucks and spikes), 15 percent of the does, and 80 percent of the fawns were removed annually for comparison with sheep management in Mendocino County, where most of the animals are marketed as lambs. The model indicated that this level of fawn removal would be excessive, as the population declined throughout the run. Sheep ranchers, in contrast, can maintain viable flocks even when 80 to 85 percent of the lambs weaned are marketed. This comparison suggests that the potential productivity of deer may not be as great as that of sheep, although additional information is needed to support this finding. The model indicates increased birth and reduced natural loss rates as deer density declines with heavy hunting removals, but the magnitude of changes in these parameters is, at present, speculative. Range losses of sheep can be held to low levels by barn lambing, supplemental feeding, medication, and other management measures considered impractical for deer. The actual level of natural losses to be expected in a deer population from which fawns are cropped heavily can be determined only by field trials.

As the population declined in run 6, the ratio of natural losses to hunting losses decreased markedly. Almost 15 deer were taken by hunting for each one dying of natural causes and the hunting kill equaled 52 percent of the July 1 population. Because of the low deer density the birth rate increased to 1.71 fawns per doe.

In run 6 the deer population was not completely exterminated even after 55 years of heavy animal hunting removals. In the real world it is doubtful whether the population could be decimated by sport hunting, as hunting pressure would decline with deer density.

Run 7

This run (25% legal buck, 15% doe, 5% spike, and 5% fawn kill) was an extension of the present bucks-only hunting in Mendocino County (run 2) to include an annual antlerless deer hunt. Therefore, the results are compared with those from run 2. The impact of the antlerless hunt was to reduce the total November 1 population from 192,977 to 171,761. The total natural losses were also reduced by 46 percent. Not only was the total kill much higher, but the legal buck kill in run 7 was 28 percent higher than in run 2 under the legal bucks-only strategy. In run 7, the natural loss to hunting kill ratio was 23 to 10, and the hunting kill was approximately 12 percent of the July 1 total population versus about 3 percent in run 2. The birth rate was similar to that of run 2, but 45 percent of the fawns survived their first year, compared with 30 percent in run 2. This increased fawn survival in run 7 resulted from reduced deer density, which corresponds in the real world to improved nutritional conditions due to reduced competition for forage.

Run 8

Run 8 (50% legal buck, 15% doe, 5% spike, and 5% fawn kill) was similar to run 7 except for an increase in the annual legal buck harvest from 25 to 50 percent. The total kill increased from 23,533 to 27,118 and the total legal buck kill increased from 7,526 to 9,727. The total November 1 population increased from 171,761 to 172,619 and natural losses increased from 54,201 to 57,183. In run 8, 14 percent of the July 1 population was removed by hunting each year, and the ratio of natural to hunting losses was about 21 to 10.

It seems unlikely that more than 50 percent of the legal bucks could be taken annually by hunters, as noted earlier, so run 8 probably approaches the maximum legal buck kill possible in Mendocino County. Comparing run 8 with run 3 (50 percent legal bucks only), the maximum legal buck kill is achieved only when does are taken as well.

Impact of combined buck and doe hunting on population dynamics. Compared to selective buck hunting, combined buck and doe hunting results in a smaller, more productive deer herd. In particular, natural losses are reduced, birth and fawn survival rates are increased, and the hunting kill is increased when both bucks and does are taken. Relative to selective doe hunting, an either sex strategy reduces total deer numbers less but produces a greater hunting kill.

The model shows that either sex hunting can increase the harvest of legal bucks above the level attainable by selective hunting of bucks only. This phenomenon has been documented in several states, such as Utah and Montana, where changes from bucks only to either sex hunting resulted in an increased buck kill along with an increase in hunter success (Reynolds, 1960; Mussehl and Howell, 1971).

Relationships Between Hunting Strategies and Hunting Pressure

The hunting strategies specified in this model are rates of removal and do not include hunter success or hunting pressure relationships. However, the results of the various strategies can be related to hunting pressure, at least in general terms.

Selective buck hunting

The number of deer hunters in Mendocino County under current hunting conditions was estimated to be about 21,000. In considering the additional hunters required for increased levels of buck removal it may be assumed that the hunting kill is related not only to the number of hunters, but to the density of legal bucks as well. The density of legal bucks determines the average area which must be hunted to locate each legal buck, provided that hunting conditions such as the length and time of the season and the bag limit are constant.

In run 2 the simulated deer population contained an average of 7.2 legal bucks per square mile at the beginning of deer season (August 1). In run 3 the numbers of legal bucks declined from run 2 to 4.5 legal bucks per square mile on August 1. Given this reduction in legal buck density, it is apparent that in run 3 additional hunters would be needed to obtain even a 25 percent rate of legal buck removal.

At the beginning of deer season, the average range area per legal buck in run 3 was 1.60 (7.2/4.5) times as large as in run 2. Assuming no increase in the amount of ground covered by each hunter, the number of hunters required to effect a given percentage removal of bucks would vary inversely with legal buck density. Therefore, the number of hunters required to remove 25 percent of the legal bucks in run 3 would be 1.60 times the number of hunters achieving the same percentage removal in run 2, or 33,600 (21,000 x 1.60).

After 25 percent of the legal bucks were taken, the density in run 3 would have declined to 3.4 legal bucks per square mile; each buck would then occupy 2.11 (7.2/3.4) times the area per legal buck at the beginning of hunting season in run 2. Again, if hunting success is proportional to the area occupied by each buck, at least 44,310 (21,000 x 2.11) hunters would be required for the additional removal in run 3 over run 2. To achieve the entire 50 percent legal buck removal in run 3, therefore, would require nearly four times as many hunters (33,600 + 44,310) in the county as at present. Associated with this increase in the number of hunters would be a drop in hunter success from approximately 0.28 bucks per hunter in run 2 to 0.10 bucks per hunter in run 3, assuming no change in the bag limit for individual hunters.

These approximate calculations indicate the magnitude of diminishing returns in hunter success to be expected as hunting pressure on legal bucks is increased. This pattern of decreasing hunter success might prevent the achievement of the 50 percent legal buck removal, due to the reluctance of hunters to participate when the expectation of success is so low. Buck hunting now occurs in August and September, the most difficult season to take bucks because of their secretive habits during hot weather. The heat also restricts the activities of hunters. Hunter success might be increased by hunting in October and November during the rut, by improving hunting access, lengthening the season, or raising the bag limit. But even if these changes produced a 50 percent harvest of legal bucks, the annual buck kill in the long run would be only slightly higher than at present due to the self-limiting nature of bucks-only hunting. Moreover, such an increase in the buck kill could be achieved only at the cost of lower hunter success and reduced trophy quality in terms of younger and smaller bucks. In the final analysis, it does not seem feasible to increase the hunting kill solely through increased legal buck removals.

Selective doe hunting

Within Mendocino County there is little experience to indicate the hunting pressure needed to achieve specified levels of antlerless deer removals. Hunter success rates in limited either sex hunts (300 permits) in a small area in the northwestern part of Mendocino County in 1963 and 1965 were 37 and 19 percent, respectively. These hunts included both legal bucks and antlerless deer as legal game. In 1971, 15 special antlerless hunts were held in various regions of California with a total of 6,959 permits sold. In these hunts 2,586 deer were taken, for a hunter success rate of 37 percent. Success rates for the individual hunts ranged from 12 to 60 percent (Inlay, 1972). Based on these data, an average hunter success rate of 37 percent is assumed for antlerless hunts in Mendocino County.

With an assumed success rate of 37 percent, about 31,000 hunters would be required to take 11,461 does annually in run 4. Thus, in terms of hunting pressure requirements, it may be feasible to control deer numbers by selective doe hunting.

Combined buck and doe hunting

While a large variety of combined buck and doe hunting removals is possible, the most likely alternative in Mendocino County would be to retain the present buck hunt in August and September and add an antlerless hunt in November. This combination was simulated by run 7 (Table 16), where the objective of the antlerless hunt was to remove conservative numbers of does. Since the current regulations in California define antlerless deer to include fawns and spike bucks with antlers shorter than 3 inches, the hunting specifications for run 7 included moderate levels of hunting on these classes as well as on does.

In run 7 the density of legal bucks at the opening of buck season (August 1) was 9.2 legal bucks per square mile, compared with 7.2 legal bucks per square mile at present (run 2). Given this greater buck density, the legal buck kill would increase from the current strategy if the number of hunters remained constant. If hunter success increased proportionally with buck density, the success rate would rise from 0.28 bucks taken per hunter in run 2 to 0.36 (9.2 /7.2 x 0.28) in run 7. With this higher success rate, the greater legal buck kill in run 7 (7,526) could be taken by the present number of hunters (21,000). However, it is likely that the number of hunters would rise because the expectation of success would be enhanced by the increased availability of legal bucks. In any case this strategy would accommodate either the current number of buck hunters at a higher success rate or more hunters at the present rate. Either alternative would raise the trophy hunting values of the deer resource above present levels.

In addition to the enhanced buck hunting, run 7 proposes an annual removal of 16,007 antlerless deer. If the success rate were 37 percent, the average for all antlerless hunts in California in 1971, a total of 43,260 antlerless permits would be needed each year.

Assuming as many buck hunters as at present, run 7 indicates total removal of 23,533 deer annually by 64,260 hunters with a success rate of 0.37 deer per hunter. This may be compared to the present harvest of 5,878 bucks (run 2) by 21,000 hunters with a success rate of 0.28 deer per hunter. On this basis run 7 represents more than a threefold increase in the number of hunters accommodated along with an increase in the success rate.

Results with Stochastic Assumptions

In all of the runs discussed to this point (Table 16), it was assumed that average forage conditions occurred in each year of each run. However, it is obvious that forage conditions vary from year to year and in this model such forage variations are simulated by the forage factor. Here, using the same set of hunting strategies as in Table 16, the variations in the deer population due to annual variability in forage conditions are illustrated. These forage variations, as simulated by the forage factor corrections, are referred to as the stochastic component of the model.

The results of the stochastic runs (Table 17) are summarized in the same format as those from the deterministic runs (Table 16) to facilitate comparisons between the deterministic and stochastic runs of comparable hunting strategies. An important feature of these results is the similarity in corresponding values throughout all the hunting strategies. The implication of this finding is that random variations do not alter the conclusions drawn from the deterministic runs. The deterministic runs are most useful for comparisons of different hunting strategies because in the absence of forage variations, the observed differences can be attributed to differences in hunting. The stochastic runs, in contrast, simulate field conditions where the effects of forage variations can be generated over time with different hunting strategies, but in the real world such forage variations complicate the comparison of various hunting strategies from different sets of years.

In addition to the eight hunting strategies repeated from Table 16, Table 17 includes an additional run (6A) for comparison with the extermination level fawn hunt (run 6). Run 6A was similar to run 6 except for a reduction in the annual fawn removal from 80 to 60 percent. This change resulted in a stable population of 134,535 deer (November 1) with an annual hunting kill twice that achieved with any other hunting strategy. Three deer were taken by hunters for each one dying of natural causes. Despite the greater number of deer taken, this policy might not be considered ideal because hunters prefer mature bucks.

An important characteristic of deer populations, as revealed by the stochastic runs, is the considerable year-to-year variability in all parameters of the population as a result of fluctuating forage conditions. Recognition of this variability is important to management because of the risk of erroneous interpretations of short-term data. Of particular interest are those parameters which are monitored in the field as a basis for management recommendations.

To demonstrate the potential variations over time in important parameters of the Mendocino County deer population, the means and extreme values for the current buck hunting strategy (stochastic run 2, Table 17) are detailed in Table 18. This run assumed the removal of 25 percent of the legal bucks in each year of the 30-year run and no long-range trend in carrying capacity. In the real world, of course, hunting and habitat conditions are rarely constant over time, even on the average. But even with these constraints, total deer numbers ranged from 169,502 to 217,224 on November 1 in various years (Table 18). The other parameters also varied widely. The maximum population occurred during or after excellent forage years (FF = 5), while the minimum was associated with poor years (FF = 1). For each parameter, the time interval between minimum and maximum values was quite short (2-6 years), indicating that the population responded rapidly to changes in forage conditions. Variations of similar magnitude occurred in all the stochastic runs, regardless of the hunting strategy in effect. The situation in a deer population at any given time reflects the total complex of environmental forces present. Both recent and carryover effects from past years may be present and it is often difficult to separate them successfully when analyzing field data.

As indicated by the coefficients of variation in Table 18, some parameters (fawn/doe ratios) are more variable than others (annual hunting kill, average age of bucks and does) in response to forage variations. It is suggested that the monitoring efforts of management should be oriented toward the most variable parameters as the best indicators of population status. This recommendation supports the current emphasis of the Fish and Game Department on herd composition counts as a primary indica-

Table 18. Variability during a 30-year simulation run with stochastic assumptions of the 25 percent legal buck hunting strategy[1]

Parameter	Mean	Minimum	Maximum	Coefficient of variation[2]	Years between max. and min.
Nov. 1 population	195,204	169,502	217,224	.07	4
July 1 population	217,886	186,353	245,339	.08	4
Annual natural losses	99,621	80,926	120,448	.11	4
Annual hunting losses	6,373	5,981	6,665	.03	6
May 1 fawns/doe	.37	.28	.52	.17	2
Nov. 1 fawns/doe	.57	.38	.76	.19	4
Birth rate (fawns/doe)	1.17	.91	1.37	.10	4
Average age (years)					
Bucks	3.10	2.90	3.42	.04	2
Does	4.83	4.64	5.07	.02	5

[1] Run 2, Table 17.
[2] Coefficient of variation = standard deviation/mean.

tion of deer herd conditions. An even more sensitive parameter, though more difficult to measure than herd composition ratios, would be the pregnancy rate of yearling does.

In view of the random variations in population parameters (Table 18), the most realistic approach to management is to pursue a selected hunting strategy over a period of years, rather than to change hunting regulations annually in an attempt to compensate for the year-to-year effects of random weather and forage fluctuations.

Model Output Compared with Hopland Field Station Statistics

Deer are hunted more heavily on the Hopland Field Station than elsewhere in Mendocino County (Table 9). The Hopland station is open to public hunting during the regular buck season and antlerless deer are collected at all seasons of the year as needed for research purposes. Run 8 (Table 16) most nearly approximates the level of hunting removals achieved at Hopland in recent years. Using the procedure of Connolly (1970), many parameters from the Hopland deer population were estimated for comparison with the output for run 8 (Table 19). Although the levels of hunting removals differed somewhat and deer density was higher at Hopland, many of the comparable parameters agreed closely. It was not feasible to simulate the Hopland strategy on the computer because

Table 19. Deer population statistics for Hopland Field Station compared with Mendocino County simulation output

Parameter	Hopland Field Station (1964-1969)	Mendocino County[1]
Annual hunting removals (%)		
Legal bucks	42	50
Spike bucks	12	5
Does	9	15
Fawns	6	5
Deer/square mile Nov. 1	92	50
Natural/hunting losses	2.1	2.1
Hunting loss/total deer July 1	.12	.14
Natural loss/total deer July 1	.25	.30
Composition of hunting kill (%)		
Legal bucks	40	35.9
Spike bucks	10	3.3
Does	32	50.4
Fawns	18	10.4
Fawns born/doe	1.12	1.19
Fawn survival to 12 months (%)	50	45
Legal bucks/doe (Nov. 1)	.17	.14
Spike bucks/doe (Nov. 1)	.22	.16
Fawns/doe (Nov. 1)	.71	.62
Fawns/doe (May 1)	.56	.55

[1] Run 8, Table 16.

the antlerless collections at Hopland are distributed throughout the year and vary somewhat from year to year, according to research requirements. Nevertheless, the comparison provides an indication of the validity of the model.

V. THE ECONOMICS OF ALTERNATIVE DEER HUNTING STRATEGIES

Because the activities of man impinge directly and indirectly on wildlife populations, there is a complex of benefits and costs associated with the conservation and management of a deer population.

Benefits of Deer in Mendocino County

The major benefits of deer in Mendocino County result from recreational uses, either hunting or nonconsumptive pursuits. Recreational value of deer has been expressed in various ways, none wholly satisfactory in a

Table 20. Estimated meat value of the average annual reported buck kill in Mendocino County, 1958-1970

Bucks taken annually[1]	Deer meat taken annually[2] (lbs.)	Possible meat value (per lb.)	Meat value per deer[2]	Value of all meat taken
4,226	232,430	$ 0.25	$ 13.75	$ 58,108
4,226	232,430	0.50	27.50	116,215
4,226	232,430	1.00	55.00	232,430

[1] From Table 3.

[2] Assuming an average carcass weight of 55 pounds as indicated by data from the Hopland Field Station.

management context (Clark, 1969). The assessment of recreational value of deer in relation to management would require a demand function encompassing both consumptive and nonconsumptive aspects and incorporating, as arguments, variables from the biosystem and hunting regulations.

The economic value of hunting can be expressed through the meat value of the venison, hunter expenditures, hunting club fees, and other economic activities associated with the handling of venison and hides. The annual value of venison taken in Mendocino County during 1958-1970 was estimated to range from 25 cents to one dollar per pound (Table 20). At a value of 25 cents per pound, an average deer carcass was worth about $13.75, while at one dollar per pound it was worth $55. Since deer meat is not sold commercially in California, it is difficult to estimate the price that consumers would be willing to pay for it.

A survey of deer hide buyers indicated a value of $1.25 per hide, or $5,283 for the average reported kill (Table 3). Tanning and manufacturing of salable hide articles also contributes to the economy. Another economic factor is the cutting and wrapping of venison for hunters by meat locker plants. The prevailing charge for these services in Mendocino County was 12 cents per pound in 1972. If 50 percent of the deer killed are processed by locker plants, the total income to these establishments in 1972 was approximately $14,000 in addition to locker rental fees.

Another measure of the value of deer hunting is the fee paid for hunting privileges on private lands. Miller and Bollman (1967) found that deer hunting clubs paid an average of $115 per year per member for hunting rights in Mendocino County (Table 21). Based on this fee and the 1.21 deer taken per member, the average expenditure per deer was $95.04. If every deer taken by hunting in the county were evaluated at this figure, the average annual buck kill during 1958-1970 (Table 3) was worth more than $400,000. Hunting fees have increased substantially since 1967 and now probably average closer to $150 per member.

Table 21. Hunting fees and kill statistics for private deer clubs in Mendocino County, 1967[1]

Hunting fees	
Average fee per member	$115.00
Highest fee per member	$250.00
Kill statistics	
Average number of deer killed per club	33.5
Average number of hunting days per club	89.0
Average number of hunters per club[2]	32.0
Average number of days to bag deer	4.45
Deer bagged per hunt[2]	1.04
Deer take per member[3]	1.21
Average value per deer	$ 95.04

[1] Miller and Bollman (1967).
[2] Includes guests.
[3] Does not include guests.

In Mendocino County in 1965, it was estimated that deer hunter expenditures exceeded 1.5 million dollars annually (Connolly, 1966). Residents of the county reported average expenditures of $164, compared with $207 for nonresidents of the county. However, many of the hunters also hunted elsewhere, so it is not possible to say that this is the value to them of hunting deer in Mendocino County.

Management and Liability Costs of Deer in Mendocino County

The direct costs of deer management include salaries of game managers and wardens and habitat improvement. The significant indirect costs result from deer damages to forests and agricultural crops, damage to fences, deer-auto collisions, competition with livestock for range forage, and transference of diseases and parasites to livestock.

Management and enforcement

The California Department of Fish and Game maintains one game manager, six wardens, and one warden captain in Mendocino County. These officers spend only a fraction of their time on deer. Salaries and other expenses devoted to big game in the county during fiscal year 1971-1972 totaled $29,021, including $17,500 for enforcement, $8,000 for management, and $3,521 for administration (Inlay, 1973).

Habitat improvement

Changes in vegetation, both accidental (as in wildfires) and deliberate (as accomplished by prescribed burning) have some effects on deer populations (Taber and Dasmann, 1958; Longhurst and Connolly, 1970).

Prescribed burning occurred on an average of about 13,000 acres annually during 1963-1966. At an estimated cost of $5 per acre, approximately $65,000 per year was spent for controlled burning during this period (Longhurst et al., 1969). However, much of this burning is aimed at the improvement of livestock ranges and hence is not totally chargeable to deer habitat improvement.

Agricultural damage

A survey of agricultural deer damage in Mendocino County in 1968 indicated approximately $43,000 damage to grapes, pears, and other fruit crops per year in addition to about $30,000 spent on damage prevention and control (Longhurst et al., 1969). Damage prevention measures including shooting, perimeter fencing, repellents, and fencing individual plants. The value of grapes increased more than 300 percent from 1968 to 1972, so the current value of deer damage to fruit crops is probably much higher than it was in 1968.

Damage to forest regeneration

A 1962 survey of damage to forest regeneration areas in the north coast region of California showed that 86 percent of the reforested acreage incurred deer damage (Lauppe, 1963). Based on a mean annual per acre increment in growth of 500 board feet for Douglas-fir and 800 board feet for redwood, an average setback of six years due to deer damage, and stumpage values of $40 per thousand board feet, the economic loss is about $23,900 per year (Anderson, 1972). However, stumpage values increased early in 1973 to $100 or more per 1,000 board feet. On this basis, the annual cost of deer depredations would amount to at least $60,000. Little effort has been expended locally to reduce forest depredations by deer because of the high cost of effective control measures.

Damage to automobiles

Deer-automobile collisions not only result in a substantial number of dead deer (Table 5) but also in a number of damaged automobiles. The estimated annual cost of repairing deer-damaged automobiles in Mendocino County alone is $75,360.[1] About 8 percent of the deer-automobile collisions result in personal injury to the occupants of the car; an average of one human death results each year.

Deer-livestock parasites and diseases

The relationships between deer and livestock in regard to parasites

[1] Twenty-nine percent of the deer-automobile collisions result in damage. The average cost of repairing the damage is $240. These data from the California Highway Patrol were reported in the *Santa Rosa Press Democrat* (Santa Rosa, Cal.), May 19, 1968.

are quite complex and are difficult to evaluate economically (Longhurst and Douglas, 1953). Certain parasite species are transferable between livestock and deer, and vice versa (Longhurst and Douglas, 1953; Baker et al., 1957). However, the economics of this problem can be evaluated only in general terms. Of the parasites and diseases common to deer and livestock in Mendocino County, the most serious economically are lungworms (*Dictyocaulus viviparus*), stomach and intestinal worms (*Trichostrongylus*, *Ostertagia*, and *Nematodirus* spp.), liver fluke (*Fasciola hepatica*), and anaplasmosis (*Anaplasma marginale*).

The thread lungworm (*D. viviparus*) is common in deer and cattle in Mendocino County but is rarely found in sheep. This parasite may kill 5 to 10 percent of the calves and produces debilitation and stunting in many more. Stomach and intestinal worms also may cause livestock losses of 5 to 10 percent annually, in addition to debilitation and weight loss. Nearly all the sheep, cattle, and deer in the county are infected (Baker, 1973). These parasites have direct life cycles and are partially host specific, so that the primary routes of transmission are intraspecific (Baker et al., 1957). Thus, the removal of deer would only marginally reduce these infections in livestock.

Liver fluke infections were responsible for the condemnation of an estimated 91,000 pounds of beef and sheep livers in Mendocino County annually during 1965-1967 (Longhurst et al., 1969). In sheep this parasite also facilitates the growth of a *Clostridium* bacillus which causes serious losses due to "black disease." Liver flukes are susceptible to control by killing the snails which serve as the intermediate host. This involves the distribution of copper sulfate on wet areas frequented by the snails and is effective regardless of the presence of deer. Thus the role of deer in fluke infections of livestock appears minimal. In fact, local fluke infections in deer have been attributed to livestock (Taber and Dasmann, 1958). On the other hand, it is possible for deer to carry flukes to previously uninfected pastures since their movements are not normally restricted by livestock fences.

In contrast to the parasites cited above, deer apparently serve as the normal reservoir for anaplasmosis. *Anaplasma* infections produce no clinical symptoms in deer or sheep but cause serious losses among cattle, particularly adult cows brought into the county from ranges where the disease is absent. Cattle raised locally acquire immunity through infection early in life when the effects are not as severe as with older animals. The presence of *A. marginale* infections in 92 percent of adult deer in this area constitutes the chief obstacle to control of anaplasmosis in cattle (Howarth et al., 1969). The tick vectors are seasonally common on both cattle and deer, and anaplasmosis is readily transmissible from deer to cattle (Osebold et al., 1959). In deer, however, *Anaplasma* infections do not appear to be density dependent. Regardless of the level of hunting removals, enough infected deer would remain to expose all the cattle in the county.

It is not possible to estimate the value of livestock losses in Mendocino County from parasite and disease relationships involving deer. The role of deer in such losses appears limited, except in the case of anaplasmosis, and seems unlikely to change significantly under any feasible hunting strategy.

Forage competition

Food habit studies at the Hopland Field Station indicated that deer are primarily browsers, with some 70 percent of their total intake consisting of the leaves and twigs of woody forage plants. The diet of sheep is nearly 80 percent grass. The diets overlap to some extent, with deer taking about 18 percent grass and sheep consuming about 7 percent browse during the year. The period of maximum dietary overlap is November through mid-April (Longhurst et al., 1969). However, the greatest competition occurs from November through January when green forage is in short supply. During this period nearly all the herbaceous feed available is used by livestock (Torell, 1972), so that deer use of grasses and forbs is in direct competition with livestock.

The diet of deer in oak woodland vegetation at Hopland consists of approximately 34 percent browse, 53 percent grass, and 13 percent forbs from November through January. If 66 percent of the daily intake of two and one-half pounds (dry weight) of forage per 100 pounds of deer body weight consists of grass and forbs, each 100-pound deer would consume 1.65 pounds of herbaceous forage per day or 151.8 pounds during the entire three-month period. On the average during 1958-1970, there was an estimated 37,500 bucks, 96,900 does, and 53,000 fawns in Mendocino County on December 1 (Table 10). The average weights of bucks, does, and fawns at this season are approximately 105, 80, and 39 pounds (unpublished data, Hopland Field Station). From these figures, the average biomass of deer in Mendocino County on December 1 was estimated at 13,756,500 pounds. Assuming that this number is representative of the entire three-month period of forage competition and that the above data are typical of the county, the deer currently eat about 20,882,000 pounds of herbaceous feed during November, December, and January. However, only about half of the county is used as livestock range, so that only 10,441,000 pounds of this feed might have been used by livestock. If this feed were replaced by hay at $40 per ton, the cost of forage competition from deer would be $208,820 per year.

Benefit-Cost Relationships of Hunting Strategies

The above estimates illustrate some of the benefits and costs associated with deer in Mendocino County. Some of these values are subject to management while others are not. The benefits are most importantly related to hunting and other recreational uses of the resource. The number of deer taken by hunters is probably one of the most indicative measures of tangible benefits. This variable is definitely susceptible to management through changes in hunting regulations. Liability costs, such as agricultural depredations and deer-auto collisions, are related to the size of the deer population and, therefore, are also susceptible to management. The benefit-cost relationships resulting from proposed changes in deer hunting can be forecast, at least in general terms.

Any hunting strategy which raises the hunting kill will increase the consumptive value of the population. Any strategy which reduces deer numbers will also reduce agricultural and forest damage, automobile damages, and competition with livestock for forage. The nonconsumptive values of the population may also be enhanced or reduced by a change in hunting regulations. A comparison of these relationships for each of the hunting strategies (Table 16) based on total deer numbers and other population statistics is shown in Table 22. Because run 6 reduced deer numbers excessively it would not be considered an acceptable strategy. Run 6A (Table 17) was therefore substituted for run 6 in Table 22. In addition to the deer population statistics the following assumptions and calculations were made.

Benefits and costs

Hunting experience. It is assumed that the hunting experience is worth $100 for each legal buck, $50 for each spike buck and doe, and $25 for each fawn. The values shown (Table 22) are based on the hunting kill from Table 16 (Table 17 for run 6A) minus 10 percent estimated cripple loss. As defined here, the hunting experience does not include the value of meat or hides, but does include license fees, hunting club fees, travel, equipment, food and other expenditures that occur regardless of hunter success.

Meat and hides. In Table 22, venison is worth 50 cents per pound. Average carcass weights: legal bucks, 55 pounds; does and spike bucks, 45 pounds; fawns, 25 pounds. Each hide is worth $1.25.

Butcher fees. This category represents payments by hunters to locker plants for hanging, cutting, and wrapping services. It is assumed that half of the deer taken by hunters are so processed, at an average cost of 12 cents per pound, carcass weight basis.

Table 22. Benefits and costs for deer hunting strategies in Mendocino County

	Hunting strategies (as in Table 16)[1]							
	Run 1	Run 2	Run 3	Run 4	Run 5	Run 6A[2]	Run 7	Run 8
Benefits ($)								
Hunting experience..	0	529,000	685,000	516,000	1,527,000	1,826,000	1,339,000	1,594,000
Meat and hides	0	152,000	197,000	245,000	578,000	853,000	513,000	597,000
Butcher fees	0	17,000	23,000	28,000	66,000	95,000	58,000	68,000
Nonconsumptive benefits	235,000	212,000	203,000	160,000	136,000	97,000	174,000	165,000
Total benefits	235,000	910,000	1,108,000	949,000	2,307,000	2,871,000	2,084,000	2,424,000
Costs ($)								
Management and enforcement	29,000	29,000	37,000	52,000	115,000	248,000	108,000	124,000
Habitat improvement	0	32,000	41,000	31,000	92,000	110,000	81,000	96,000
Agricultural damage	152,000	150,000	149,000	121,000	118,000	75,000	133,000	132,000
Forest damage	61,000	60,000	60,000	48,000	47,000	30,000	53,000	53,000
Automob le damage	75,000	75,000	75,000	58,000	58,000	52,000	67,000	67,000
Forage competition..	220,000	207,000	202,000	172,000	149,000	95,000	172,000	164,000
Total costs	537,000	553,000	564,000	482,000	579,000	610,000	614,000	636,000
Net annual value ($) ..	– 302,000	+357,000	+544,000	+467,000	+1,728,000	+2,261,000	+1,470,000	+1,788,000
Net value relative to run 2	–0.9	1.00	1.5	1.3	4.8	6.3	4.1	5.0

[1] Table 17 for run 6A.
[2] Run 6A substituted for run 6 (see text).

Nonconsumptive benefits. Legal bucks are believed to have greater aesthetic value than spike bucks, does, or fawns. Nonconsumptive values for the current strategy (run 2) were set arbitrarily at $2 per legal buck and $1 per antlerless deer present in the population on November 1. In considering changes in nonconsumptive values under strategies other than run 2, constant values per deer could not be assumed because deer become hard to observe at low densities. Because of the reduced likelihood of deer being seen by tourists, the value of each individual deer decreases as deer numbers decrease. This factor was considered in Table 22 by adjusting the value of individual deer in proportion to the November 1 density.

To illustrate, in run 2 the population contained 18,718 legal bucks and 174,259 other deer on November 1. At a value of $2 per legal buck and $1 per other deer, the nonconsumptive value of this population was $211,695. In run 1 and run 3 the November 1 density was 56 deer per square mile, just as in run 2. In runs 1 and 3, therefore, the values for each legal buck and antlerless deer remained at $2 and $1. In run 4 the density was 43 deer per square mile, 77 percent (43/56) of the density in run 2, so the value of each legal buck declined to $1.54 (.77 x $2) and each antlerless deer was worth only $0.77. Values for the other runs were calculated similarly. Run 1 shows the highest nonconsumptive value because of high density and large numbers of legal bucks; run 6A had the lowest value because of lowest density and few legal bucks in the population.

Management and enforcement. Management costs are fixed administratively by the Fish and Game Department, and therefore may vary independently of deer numbers or hunting strategies. Such costs under the current strategy (run 2) were $29,000 per year during 1971-1972. In Table 22 it was assumed that these management costs would not change if hunting were curtailed (run 1). In other runs, management costs were assumed to rise in proportion to the hunting kill, reflecting increased enforcement needs and an expanded monitoring program.

Habitat improvement. Earlier it was estimated that $65,000 per year was spent for controlled burning in Mendocino County, but much of this burning is aimed at the improvement of livestock ranges. In Table 22 it was assumed that half the controlled burning (run 2) is done for deer range improvement. If hunting were stopped (run 1) there would be little incentive for deer habitat improvement. With changes in hunting, however, changes in burning expenditures were forecast in proportion to the increased value of the hunting experience, presuming that improved hunting opportunity would stimulate an increase in habitat improvement work.

Agricultural damage. The level of agricultural damage and damage prevention activities from deer was estimated to be $73,000 per year in 1968. Because of increased crop values and fencing costs, deer depredations now probably exceed $150,000 annually. Using this value for run 2, the cost of agricultural damages for other runs was assumed to be proportional to deer density on May 1. Agricultural depredations occur mainly during the late spring and summer months.

Forest damage. The current annual cost of deer damage to forest tree seedlings was previously estimated at $60,000. In Table 22 this value was taken for run 2 and adjusted proportionally with May 1 density for the other runs.

Automobile damage. The annual cost of repairing deer-damaged automobiles in Mendocino County was estimated previously at $75,360. This estimate was used for run 2 and adjusted proportionally with deer density on November 1 for the other runs.

Forage competition. The cost of the competition between deer and livestock for forage was previously estimated to be $1.59 for each buck, $1.21 for each doe, and $0.59 for each fawn in the population on December 1. These values were used to calculate the costs of forage competition (Table 22). The results suggest a substantial reduction in the cost of forage competition in each run where an antlerless hunt occurred.

No values are shown in Table 22 for the costs of livestock parasites and disease losses involving deer. The magnitude of such losses would not be expected to change greatly as long as substantial numbers of deer are present.

Benefit-cost estimates

The benefit-cost estimates proposed in Table 22 indicate that the net value of the deer population in Mendocino County could range from –$302,000 to +$2,261,000 annually, depending upon the hunting strategy. In comparison with these values, agricultural production in the county in 1971 was worth approximately $22 million (Eriksen, 1972). Timber production, in terms of saw logs delivered to mills, totaled $37 million in 1970 (Passof, 1971). Thus, the economic potential for deer management is small in relation to other natural resources. However, the net value of the deer resource could be increased substantially above the present level by changing to an antlerless hunting program. The values in Table 22 are based on a variety of assumptions, each subject to argument. The calculations, however, can be repeated using other assumptions as the situation requires.

The analysis of Table 22 suggests that the greatest change in the net value of the deer population resulting from changes in hunting regulations would occur in the area of consumptive benefits, i.e., the increased value of sport hunting. Compared to this potential increase, the possibilities for reducing damage costs by changing hunting regulations appear relatively minor. Certain portions of the county could be subjected to heavier hunting to reduce damage if this were desirable.

The analytical method proposed here can be used to develop a deer hunting strategy which maximizes the net value of the resource to society. The strategy, however, would be contingent upon agreement by all segments of society as to the monetary value of each benefit and cost relative to the most desirable management objectives. Such agreement would be difficult to achieve, not only because of philosophical differences regarding the value of intangible benefits, but because the costs and benefits of the deer resource are not equally distributed through our society.

VI. SUMMARY AND CONCLUSIONS

Deer management is the manipulation of a deer population and its environment in an attempt to satisfy a set of objectives. The objectives typically include economic and social as well as biological considerations. Deer numbers are also affected by environmental variations beyond the control of managers and usually cannot be determined with great certainty. Thus, the effects of management decisions may at times be unpredictable and often undetectable. Deer are owned collectively by all the people of the state, and the management problem is compounded by the political influences of sportsmen, preservationists, ranchers, timber growers, and other special interest groups.

The land use pattern in Mendocino County influences the deer population in numerous ways. In recent years, logging temporarily improved the deer habitat in much of the county, but deer depredate forest tree seedlings as well as agricultural crops. Deer are attractive to tourists but also constitute a traffic hazard. Mendocino County supports more deer hunting in the early deer season than any other California county. Deer not only compete with livestock for forage but harbor parasites and diseases injurious to livestock. Average deer numbers in Mendocino County were estimated at approximately 190,000 animals (November 1), and appear to be primarily limited by the carrying capacity of the habitat, especially the available food supply. Both quantitative and qualitative food shortages exist at various seasons.

The computer simulation model presented in this report characterizes the deer population in Mendocino County as a dynamic, density-dependent birth and death process. Birth rates are defined in the model as a function of deer density at the time of conception each year (November

1). Deer losses result either from hunting or natural causes (including all causes but hunting). The natural mortality rates for each age and sex class in each month are defined as a function of deer density. In the calculation of births and natural losses, deer density is used as a proxy variable encompassing environmental influences of the density-dependent type. For each run of the model, hunting removals are specified in the desired months as proportions of the inventory in each age and sex category to be taken by hunters. In the model, hunting can occur in any combination of sex and age classes in any month or combination of months.

The real biosystem is subject to random variations from changes in weather and forage conditions. In the model, these random components are represented by a proxy variable called the forage factor which simulates the probability and magnitude of annual variations in forage quality-quantity conditions. The forage factor can be suppressed, permitting runs based on average conditions each year. Though the model simulates year-to-year variations in forage conditions, it assumes no long-range trends in carrying capacity.

The data used in the model are from the California Department of Fish and Game records for Mendocino County and the records for the deer population on the Hopland Field Station of the University of California in the southeastern part of the county. These data were compiled, critically reviewed, and transformed into a format consistent with the structure of the simulation model. After using these initial estimates in validity checks of the model, the data assumptions were reviewed and revised. This model validation phase of the simulation was continued until the biologists considered the model adequately representative of the Mendocino County deer population.

The simulation model described in this bulletin can be used to investigate any desired hunting strategy. However, the options of the wildlife manager are limited for various practical reasons. The results of eight hunting strategies, representing the range of feasible options in Mendocino County, demonstrated several important biological principles pertinent to deer management:

1. In the absence of hunting, or when bucks are hunted selectively, deer numbers oscillate around an upper limit defined by the carrying capacity of the habitat.

2. Selective hunting of legal bucks alone as currently practiced in Mendocino County has virtually no effect on total deer numbers, compared to a no hunting strategy, but does affect the relative proportion of bucks and does in the population.

3. With selective buck hunting, natural losses are greater than they would be with no hunting at all. As the intensity of selective buck hunting

increases, the sex ratio of the population shifts toward fewer bucks and more does. The reproductive performance of individual does does not change, so the number of fawns born (and dying) each year increases as the number of does increases with selective buck hunting. This conclusion assumes that the carrying capacity would be the same regardless of the hunting strategy in effect.

4. Selective hunting of does, even at moderate levels of harvest, causes a marked reduction in total deer numbers. In situations where deer numbers must be reduced, antlerless deer hunting is required. However, a moderate reduction in numbers will increase productivity through reduction of competition for forage.

5. The legal buck kill cannot be maximized by limiting hunting exclusively to legal bucks. Antlerless hunting increases the potential legal buck kill by increasing the rate of survival of male fawns to adulthood.

6. The maximum hunting kill (numbers of animals) would be achieved by heavy hunting removals of bucks and fawns and a moderate harvest of does.

7. Regardless of the hunting strategy in effect, the hunting kill and all other population parameters will vary from year to year in response to random climatic fluctuations. In evaluating field data, managers should distinguish carefully between the effects of hunting and other environmental influences on the population.

8. As the deer population fluctuates with forage and other environmental variations, some parameters of the population exhibit more variation than others. The population parameters currently monitored in Mendocino County include the hunting kill and fawn/doe ratios. Of these two parameters, fawn/doe ratios are more variable, and therefore provide the most sensitive index to the status of the population.

From benefit-cost comparisons of various hunting strategies, it is shown that the net value of the deer resource to society could be materially increased by liberalizing hunting regulations. Depending upon the numbers of deer taken, antlerless hunting would tend to reduce forest and agricultural depredations, deer-auto collisions, and other liability costs. However, the major economic impact of antlerless hunting would result from the increased value of hunting benefits.

This report has shown that computer simulation is a valuable tool for studying the effects of hunting on deer populations. The simulation methodology, which permits the synthesis of fragmentary data and ideas into a model biosystem, leads to conclusions not readily apparent from more conventional methods of analysis. With appropriate modifications this model could be applied to other big game populations.

From our conclusions it is apparent that the management policy objectives of the State Fish and Game Commission for deer in California are not being achieved in Mendocino County. It is our hope that this report will contribute toward the better achievement of those objectives.

APPENDIX

Three computer runs of 30 years are compared with field data in Appendix Table 1. These runs illustrate the improved agreement between the computer output and field data resulting from corrections and revisions in the input data.

Run 1

Comparing the output summary with field data the average November fawn/doe ratio of .71 was higher than the expected value of .60. The coefficient of variation of 31 percent also exceeded the value of 19 percent computed from field data. In addition, the range of the November fawn to doe ratios was much wider than that observed in the field. From these comparisons it was obvious that fawn production and/or survival in run 1 was too high and too variable.

In reviewing the input data for run 1 it was recognized that variations in the fawn to doe ratio result from variations in births as well as deaths. However, in run 1 the forage factor corrections to natural mortality were specified to give the required variability with births held constant, even though variability in births was also explicitly related to the forage factor. These two sets of corrections compounded to give excessive variability in fawn production and survival.

A second discrepancy noted in run 1 was that the mean November buck to doe ratio was higher and less variable than expected. In connection with this high buck to doe ratio, the average buck kill in run 1 also was higher than expected. The kill in the model should be higher than indicated by field data because the model includes unreported kills and cripple losses. But if the reported kill of 4,226 is increased 50 percent to include the estimated cripple loss and unreported kill, the resulting total kill estimate of 6,339 is still lower than that indicated by run 1. The excessively high buck to doe ratio was apparently due to the specified 50:50 sex ratio for yearling deer.

The above results indicated that the input data including parameter values for run 1 required revision. For run 2 the forage factor correction for birth and natural mortality rates were revised to reduce the variability in the fawn to doe ratios.

Run 2

The changes in FF corrections for birth and natural mortality rates reduced the November fawn to doe ratio from .71 to .66 and also reduced the variability of this parameter. Both these statistics are larger than desired but the changes were in the desired direction, indicating further modification. These changes produced only minimal effects on the November buck to doe ratio and the hunting kill. For run 3, therefore, further modification of the FF corrections was made and, in addition, the fraction of yearling fawns which are males was reduced from 0.5 to 0.4.

Run 3

The data change from run 2 to run 3 reduced the November fawn/doe ratio to .56 with a coefficient of variation of 20 percent compared with the field data values of .60 and 19 percent, respectively. The reduction of the yearling sex ratio from 50 to 40 percent males reduced the total kill as desired and reduced the November buck/

Appendix Table 1. Validation runs of the Mendocino County deer model

Parameter	Run 1[1]	Run 2	Run 3	Field data average of 1958-1970[2]
November fawn/ doe ratio				
Mean	.71	.66	.56	.60
Coefficient of variation (%)	31	28	20	19
Range of values	.37 to 1.10	.42 to 1.06	.38 to .76	.41 to .77
November buck/ doe ratio				
Mean	.43	.42	.29	.27
Coefficient of variation (%)	8	10	5	26
Range of values	.36 to .47	.28 to .50	.26 to .32	.17 to .37
Annual buck kill[3]				
Mean	7,789	7,531	5,859	4,226
Coefficient of variation (%)	9	12	7	10
Range of values	6,277 to 8,874	4,164 to 9,008	5,314 to 6,620	3,315 to 4,869

[1] The same hunting strategy of removing 25 percent of all legal bucks each year was used for run 1, run 2, and run 3.

[2] Field data do not include cripple loss or unreported kill; these are included in run 1, run 2, and run 3.

[3] From Tables 3 and 4.

doe ratio to .29, compared with the field estimate of .27. However, the variability of this parameter is still low compared to the field data. It is possible that the field data overestimate the variability of buck/doe ratios because the herd count may not coincide exactly with the rut each year and bucks are most likely to be observed during the rut. Another possibility is that the yearling sex ratio may vary annually, even though in the model it is held constant throughout a run. The sex ratio of deer at birth has been shown to vary with range quality (Verme, 1969). Recent calculations with herd composition data from the Hopland Field Station suggest that the sex ratio of yearling deer is variable from year to year. If the yearling sex ratio was changed in the model from a constant to a variable, the variability of the buck to doe ratios would increase.

After evaluating the results of run 3, it was concluded that the model adequately represented the deer population of Mendicino County, so far as could be ascertained from available data. Accordingly, we proceeded to experiment with alternative hunting strategies.

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