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Population Dynamics and Age Determination for Five Utah Deer Herds

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POPULATION DYNAMICS AND AGE DETERMINATION

FOR FIVE UTAH DEER HERDS

by

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of the requirements for the degree

of

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ABSTRACT

Population Dynamics and Age Determination

for Five Utah Deer Herds

by

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Utah State University, 1976

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Ages of 213 deer killed during the 1972 hunting season were determined by: (1) eruption-replacement and wear criteria in the field: (2) employing the tooth eruption-replacement and wear criteria under optimum laboratory conditions; and by (3) cementum-annulation counts. Incisors collected for cementum-annulation counts were decalcified in 5 percent nitric acid, sections 16-18 microns were cut on a cryostat and stained in hematoxylin for 18 ± 2 minutes. Age determinations by cementum-annulation counts showed 87 percent agreement with the results obtained by eruption-replacement and wear criteria in the laboratory.

Survival rates were estimated from the age distribution of 740 teeth aged by cementum-annulation counts. The average adult doe survival rate was 0.55. Other population parameters were also determined. All five deer herds showed apparent negative rates of population change, averaging -0.14. The adult female survival rate appeared to be the major source of variation between units in rate of population change. The correlation between hunting pressure and the rate of population change was statistically significant.

(49 pages)

INTRODUCTION

Justification

The goal of most programs designed to manage deer populations for sport hunting is to maintain the largest possible healthy herd which can remain at equilibrium with its food base and is compatible with other land uses. Ideal attainment of this goal requires a knowledge of the vegetation in terms of the browsing pressure and number of deer which it can currently support as well as trends in plant succession; and of deer demography in terms of reproductive and mortality rates, and the effects of various exploitation levels on that demography. If the equilibrium population level, and that harvest rate which annually removes the reproductive increment can be ascertained, a herd can potentially be cropped on a sustained-yield basis, provided hunting regulations can be set which produce the desired level of kill while allowing for natural decrements.

Several states have attempted to achieve this pattern of population management. Wisconsin (Doll and Creed 1961), Michigan (Bartlett 1960) and Pennsylvania (Forbes 1961) have subdivided their states into herd units and attempted to estimate actual deer numbers in these units; and knowing the annual reproductive increments in those populations, promote a variety of hunting regulations to attain a harvest which just crops the increment. Bartlett (1960) stated that the winter mortality has been reduced and the herds are healthier since the implementation of sustained-yield harvests in 1952. Michigan deer hunters harvest approximately 100,000 deer annually. The elk-harvest program in Utah described by Hancock (1955) and Kimball and Wolfe (1974) may serve as a model of this type of population management.

Presently the formulation of deer-harvest policies and hunting regulations in Utah, as in many other states, are based heavily on indices of the occupancy and use of winter deer range: notably pellet-group counts, browse-utilization measurements (Cole 1959), and spring trend counts. Since the length and intensity of winter-range use are largely a function of the length and severity of the winter, these indices reflect range occupancy as much as, if not more, than actual deer numbers. It may be true that the mean browse-utilization rate and pellet-group counts may be higher over an extended period with high deer densities than in a similar period with low densities. However, inter-annual variations in such indices probably reflect variations in winter weather rather than actual changes in deer numbers. Hence, they would seem to be a questionable basis for annual decisions on harvest levels. These reservations have been corroborated empirically by Mackie's (1976) findings in Montana. He concluded that browse surveys should be used cautiously, if at all, in relating past or present ungulate population trends to range conditions.

The state is also in a transitional period in terms of other forces affecting the formulation of hunting regulations. Up to the 1960's, deer numbers were large and hunter numbers relatively small. Liberal hunting regulations could be accommodated annually with either-sex seasons providing high rates of hunting success.

However, as the state's population has grown during the past two decades, hunter numbers have now reached the point where either-sex harvests have increasingly exceeded reproductive increments and herd trends have apparently been downward for some time.

The state is now in a stage where alternating, either-sex and buck seasons will produce a similar pattern to that experienced in eastern and midwestern states some 20 years ago: years of high success and herd reduction, and years of low success and herd recovery. The result will be one of alternate hunter pleasure and displeasure, and "boom or bust" hunting seasons.

Here again, it would be far more desirable in terms of the quality and professional stature of the management program and public relations considerations, to implement a sustained-yield harvest scheme approaching the sophistication of the Utah elk-harvest program.

In order to accomplish this goal, it will be necessary to measure the demographic patterns of Utah deer herds in terms of reproductive and mortality rates so that harvest rates which will stabilize herd size can be calculated. This project was initiated to measure mortality rates of five Utah deer herds, compare these rates with observed recruitment rates, and calculate population trends of these herds.

Since mortality rates were to be estimated from age distributions obtained from hunting season samples, it was necessary to develop, and apply to Utah data, aging techniques with which each animal could be assigned to a year-class rather than the currently used age classes (fawn, yearling, 2.5 year-old, mature, and old). The technique used was that of counting cementum-annulation layers as discussed by Klevezal' and Kleinenberg (1967), Low and Cowan (1963).

Life-table analyses as described by Quick (1963), Eberhardt (1969), Seber (1973) and numerous other authors, remain a standard method of estimating mortality and survival rates. However, they have been supplemented by techniques such as those described in Robson and Chapman (1961) for estimation of survival rates. One advantage of the latter method is that it permits calculation of the variance of the survival-rate estimate. Robson and Chapman also provide iterative means of treating age distributions which are not completely geometric, sampling errors in segments of the population, especially among the older age classes. Henny et al. (1970) have described a model for calculating population parameters necessary to maintain a stable population. Their model is based on the matrix approach to population analysis, as described by Leslie (1945, 1948), Pielou (1965) and others. It requires a knowledge of: (1) age-specific survival rates; (2) the age at which the species reaches maturity; and (3) the recruitment or age ratio of the population. Analysis by the Robson and Chapman and Henny et al. techniques are valuable in understanding the mechanics of population maintenance.

Age determination for mule deer (*Odocoileus hemionus*) in Utah is currently based upon the sequence of tooth eruption and replacement and patterns of mandibular wear (Robinette et al. 1957). The validity of age determination by patterns of mandibular wear has been questioned by Erickson et al. (1970) and Gilbert and Stolt (1970). Deer-eating woody vegetation might exhibit greater tooth wear than those eating herbaceous vegetation. The rate of wear also depends upon the amount of abrasive material on the vegetation upon which the deer feed. Severinghaus and Cheatum (1956) found that the white-tailed deer (*Odocoileus virginianus*) from the dusty areas of Texas exhibited approximately twice the degree of wear as those of the same age from New York. Varying habitat, vegetation and soil conditions within Utah could produce different wear patterns for mule deer in various regions of the state.

Cementum-annulation counts have proven to be reliable age determinants for many mammalian species (Klevezal' and Kleinenberg 1967) including mule deer (Low and Cowan 1963). Research by the latter authors revealed that the number of cementum annulations was directly related to the animals' actual age. The number of cementum annulations was free from environmental influences such as sand and grit on the browse and the texture of the browse. In addition to decalcification, sectioning and staining the teeth, Low and Cowan's procedure required that the teeth be dehydrated, infiltrated by immersion in an ethanol series, cleared in benzene and then imbedded in Tissuemat. The procedure required over 40 hours between decalcification and sectioning. Allen and Collins (1971) described a simplified procedure in which teeth were sectioned by means of a cryostat. This process eliminated much of the time required for tooth preparation, thus making cementum-annulation counts feasible for large-scale operations.

During the 1971 hunting season, approximately 200 incisors were collected by Utah Division of Wildlife Resources (UDWR) personnel and Utah State University students at deer checking stations in Blacksmith Fork and Logan Canyons, Cache County, Utah. A preliminary comparison of various histological techniques employed in tooth processing was made in terms of time required, cost of materials, and quality of the sections obtained. Based on this comparison, the process described below under PROCEDURES was employed in the 1972 study.

Objectives

1. To estimate mortality (or survival) rates of five Utah deer herds, and with observed recruitment rates, calculate rates of population change in these herds.

2. To relate calculated population trends to demographic variables and environmental influences in an attempt to explain their magnitude.

3. To develop age criteria based on cementum-annulation counts so that age structures subdivided by year-class groups could be measured and permit survival estimates.

4. To compare accuracy and cost of aging by cementum-annulation counts, and the presently used tooth-eruption, replacement, and wear technique.

PROCEDURES

Study Areas

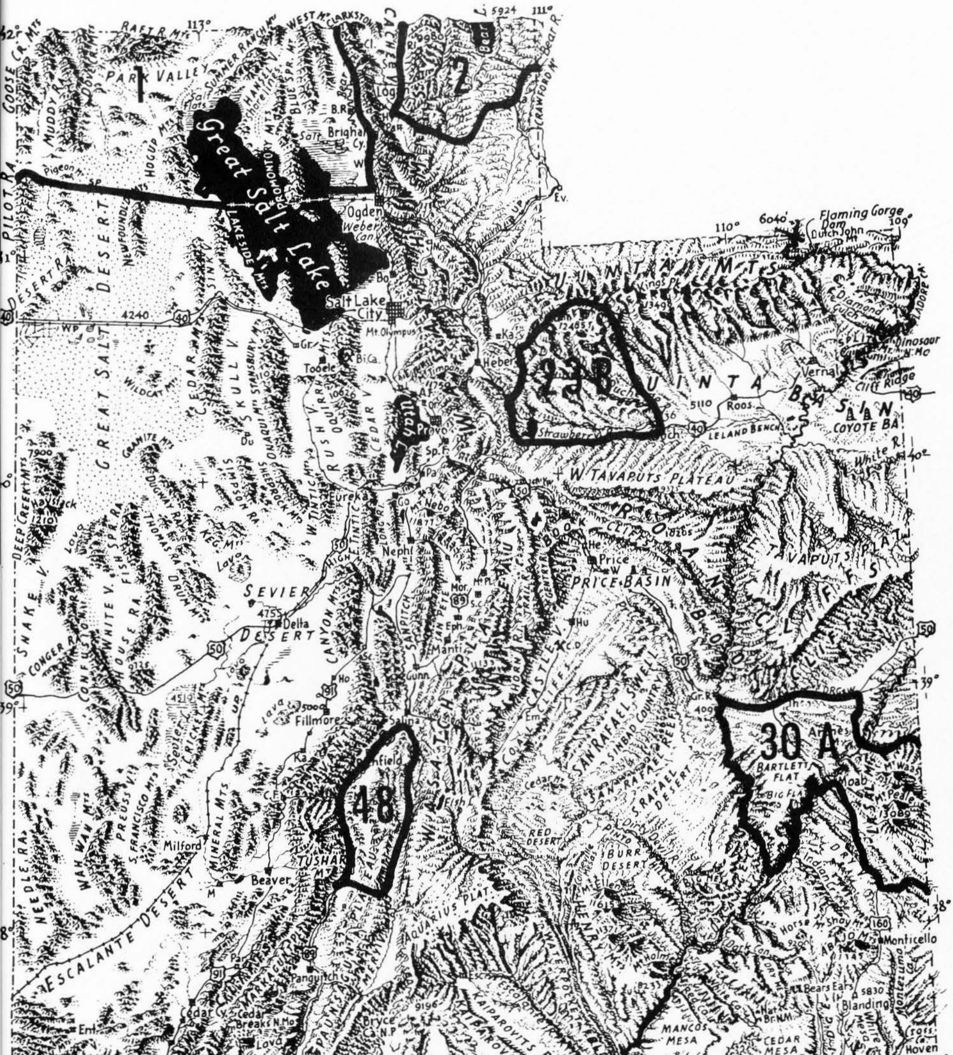
Prior to the 1972 hunting season, personnel of the UDWR selected five herd units which had checking stations manned each year during the deer-hunting season for this study. The units selected were Box Elder (Unit 1), Cache (Unit 2), Strawberry-Currant Creek (Unit 23B), LaSal Mountain (Unit 30A), and Monroe (Unit 48). Location and major topographic features of these units are shown in Fig. 1. Other characteristics of the units are compared in Table 1.

Field Age Determination and Collection of Incisors

During the course of examining deer brought in by hunters to the checking stations on the five study units, UDWR personnel selected a total of 213 animals at random. Fawns were excluded from the sample because they can be aged by dentition, i.e. milk incisors. Each of these animals was assigned an age according to their usual field-aging technique. The mouth of each animal was cut with a knife from its corner back to the base of the jaw. The jaws were then pried open widely enough so that all teeth could be seen. Age was assigned, on the basis of tooth eruption-replacement-and-wear criteria, to one of five age classes: fawn, yearling, 2.5 year old, prime (3-6 years) and old.

Each of the 213 animals was assigned a number, and its field-determined age recorded. The lower jaw of each of these animals was then removed and marked with its assigned number. The incisors were

Figure 1. Location and topographic features of the selected deer herd units; Box Elder (1), Cache (2), Strawberry-Currant Creek (23B), LaSal Mountain (30A), Monroe (48).



Great Salt Lake
Salt Lake City
Ogden
Tooele
Provo
Utah L.
Eureka
Nephi
Delta
Fillmore
Richfield
Milford
Beaver
Panguitch
Cedar C.
Cedar Breaks N.Mo
Zion N.P.
St. George
Kanab
Bryce C.N.P.
Heber
Vernal
Roos.
Price
PRICE BASIN
Moab
Monticello
Blanding
Salina
Manti
Gunn.
Flaming Gorge Dam
Dutch John
Dinosaur N.Mo
PARK VALLEY
GREAT SALT DESERT
SEVIER DESERT
ESCALANTE DESERT
UINTA BASIN
W TAVAPUTS PLATEAU
SAN RAFAEL SWELL
SINBAD COUNTRY
SAN RAFAEL DESERT
BURR DESERT
RED DESERT
MANCOS MESA
CEDAR MESA
KAIPAROWITS BASIN
AQUARIUS PLAT.
PINK CLIFFS
WHITE CLIFFS
VERMILION CL.
BARTLETT FLAT
COYOTE BA.
LELAND BENCH
Cliff Ridge
Monument V.
Gothic Mesas
Rainbow Br.
Virgin R.
White R.
Bear R.
Mt. Olympus
Mt. Nebo
Bears Ears
San Juan
1
2
23 B
30 A
48
113°
112°
111°
110°
109°
114°
39°
38°

Table 1. Summary of range areas and elevations, hunting pressure, and major vegetation types for the five units

	Unit				
	1[a]	2[a]	23B[b]	30A[c]	48[d]
Winter range					
Area (km^2)	2620	282	1310	1000	590
Elevation (m)	1500-2500	1500-2300	1750-2700	1500-2700	1650-2500
Summer range					
Area (km^2)	394	1880	2110	2120	700
Elevation (m)	2400-3200	2400-3700	3000-4200	2600-4000	2800-3420
Ratio of summer range area: winter range area	0.2	6.7	1.6	2.1	1.2
Average number hunters per km^2	0.9	3.9	2.2	1.3	3.2
Major vegetation types on the winter range	Sagebrush-juniper, sagebrush, and juniper	Sagebrush, mixed browse, and juniper	Pinyon-juniper-sagebrush-grass, pinyon juniper-mountain brush, and sagebrush	Pinyon-juniper and desert shrub	Pinyon-juniper

[a]Source: King and Muir (1971)
[b]Source: Huff and Coles (1966)
[c]Source: Coles and Pederson (1968)
[d]Source: Huff and Blotter (1964)

extracted by UDWR personnel for later age determination by cementum-annulation counts, and placed in bags with numbers corresponding to the jaws from which they came. The jaws were used for a later age determination, in which tooth eruption-replacement and wear criteria were employed under optimum laboratory conditions. An additional 517 incisors were collected by UDWR personnel and Utah State University students. These incisors were collected to increase sample size for population analysis.

Incisors were removed at the checking stations by cutting into the gum material (Fig. 2) on the distal sides of I_1 and I_2. The cuts were deep enough to ensure that the root tips would not be broken during extraction. After the two cuts were completed, the two first incisors were extracted with pliers (Fig. 3) by pressure on the lingual side. The incisors were stored dry for short periods. Teeth that cannot be processed within a month should be stored in a 10 percent formalin solution.

Tooth Preparation and Aging

Age determination by cementum-annulation counts on histological sections required decalcification and sectioning of the incisors, and staining and mounting of the sections. Preparation of incisors was similar to the procedures described by Allen and Collins (1971) and Miller (1974).

Incisors were decalcified in a 5 percent solution of concentrated nitric acid. Approximately 75 ml of solution were used per incisor. Best results were obtained when the solution was changed twice daily. When decalcification was complete the teeth were slightly yellow and very flexible.

Figure 2. Cutting of gum material prior to extraction. A small-bladed knife is used to cut gum material to facilitate extraction of teeth.

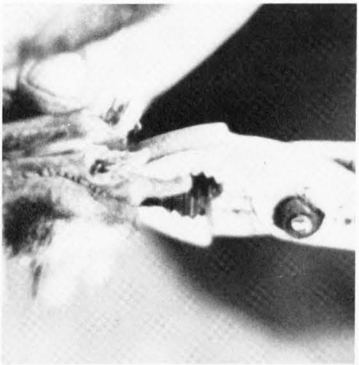


Figure 3. Teeth extraction with pliers. Note that the pliers tip extends beyond the tips of the teeth.

A chemical test was made prior to each solution change to determine whether decalcification was complete. This involved drawing 5 ml of the decalcifying solution from the bottom of the container and adding 5 ml each of 5 percent ammonium hydroxide and of 5 percent ammonium oxalate to the solution. After mixing, the solution was allowed to stand for 10 minutes. A cloudy solution indicated that the teeth were not completely decalcified, whereas a clear test solution indicated that no additional decalcification was required. The decalcified teeth were rinsed in running tap water for 12 or more hours and then stored in distilled water or 5 percent formalin solution.

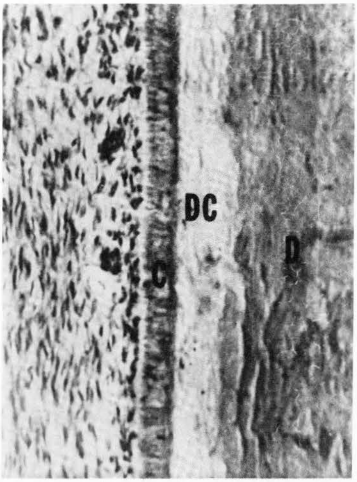
Decalcified teeth were sectioned as soon as possible, since section quality deteriorated when decalcified teeth were stored longer than 2 weeks. The teeth were sectioned longitudinally along the buccal-lingual axis at 16-18 microns on a cryostat at -30° C. The sections were removed from the cryostat by slight contact with a warm dry slide and were smoothed by placing a drop of water on each section. Four sections were placed on each slide. Drying the slides on a slide warmer at 40° C for 1-2 hours improved adherence of the section to the slide.

The sections were then stained in full strength hematoxylin for 18-20 minutes, dipped in distilled water to remove excess stain, dehydrated in an ethanol series (50 percent EtOH for 2 minutes, 75 percent EtOH for 1 minute, and 90 percent EtOH for 1 minute) and finally cleared in a solution of 75 percent amyl acetate and 25 percent cedarwood oil. The slide coverslip was mounted with a synthetic mounting medium.

Age was determined by counting the cementum annulations and adding 1.5 years (Low and Cowan 1963). The first cementum rest line appears in the permanent incisor during the deer's second winter, and thus is not present in incisors of yearling mule deer (Fig. 4). Figure 5 illustrates a section of a tooth from a 6.5 year-old mule deer.

In addition to the tooth aging, the jaws were examined in the laboratory. Ages were assigned by the UDWR personnel to each on the basis of tooth-eruption-replacement and wear criteria.

After the cementum-annulation counts and laboratory age determination were completed, the results of the three age determinations (these plus field age determination) were compared. Agreement rates were calculated from the comparison results. The incisors of the animals aged incorrectly (i.e. disagreed with laboratory age determination) were re-examined to determine the source of error. Records of man hours and material costs for the cementum-annulation count age determination versus field age determination were also maintained.



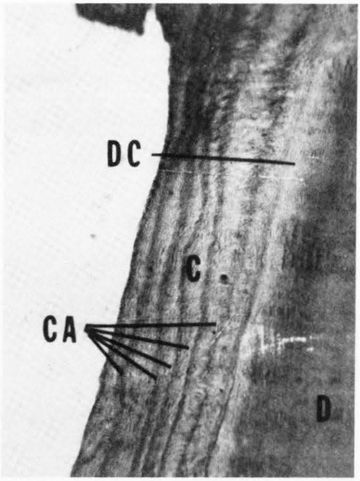


Figure 4. Longitudinal section of yearling mule deer incisor. D - dentin; DC - dentino-cemental interface; C - cementum. (100x)

Figure 5. Incisor section of 6.5 year-old mule deer. D - dentin; DC - dentino-cemental interface; C - cementum; CA - cementum annulation. (150x)

Population Analysis

The age structure of each deer herd was estimated from the age frequency distribution obtained from cementum-annulation counts. The sample sizes were 134, 249, 122, 96, and 135 for units 1, 2, 23B, 30A, and 48, respectively. Adult survival rates were calculated by the procedure described in Robson and Chapman (1961). Henny et al. (1970) have outlined procedures for determining: (1) necessary production for maintenance of a stable (constant numerical strength) population; (2) required age ratios in a population which yield a stable population;

and (3) annual rate of change in population size assuming constant survival and reproduction.

In an attempt to explore the relative importance of various parameters as determinants of the rate of population change, correlation coefficients were computed between the estimated rate of population change and: (1) adult female survival rate; (2) adult male survival rate; (3) recruitment; (4) the ratio of summer to winter range areas; and (5) an index of hunting pressure.

RESULTS AND DISCUSSION

Comparison of Aging Techniques

Accuracy comparison

Age classes, as determined by cementum-annulation counts showed 82.5 percent agreement with the laboratory age determination (175 of 213 samples agreed) while field aging showed 79 percent agreement with the laboratory age determination. Cementum-annulation counts showed an 87 percent accuracy when the laboratory-aged yearling jaws were used as known-age specimens. The yearlings may be considered known-age animals, because schedules of eruption and replacement deviate only under extreme conditions (Taber 1969).

The actual tendency was to place older animals into younger age classes with cementum-annulation counts while the opposite was observed in field aging (Table 2). The age classes, as determined by cementum-annulation counts, were significantly different from the laboratory aging ($\chi^2_{.05}(2) = 5.99 < 16.98$) while field aging was not significantly different from the laboratory aging ($\chi^2_{.05}(2) = 5.99 > 2.71$).

While the sources of error for the field aging could not be ascertained, those for the cementum-annulation counts were categorized. Of the 38 animals incorrectly aged by cementum-annulation counts: (1) 26 percent (10 specimens) were attributed to errors in transcribing the number assigned to each tooth since the cementum-annulations were distinct and clear, making the aging discrepancy improbable; (2) poor quality slides accounted for 28 percent (11 animals); and (3) actual error in age determination was 46 percent (17 specimens).

Table 2. Results of the comparison of age-determination methods

Age class	Age (years)	No. animals assigned to each age class by method			
		Cementum-annulation count		Lab aging	Field aging
II	1.5	64		57	51
III	2.5	72		51	45
IV	3.5	46			
IV	4.5	25			
IV	5.5	4	76	105	117
IV	6.5	1			
V	7.6	1		0	0

A major advantage of the cementum-annulation count is that the ages are determined to a year class not an age class. Subdivision of age distributions into year classes is necessary for mortality estimates and the subsequent population analyses attempted in this report.

Cost comparison

The cost of field material for field aging was approximately $1.00 per 100 animals aged. This amount covered jawbars, knives, record sheets and other items required for field aging. The cementum-annulation count field material cost was approximately $2.00 per 100 animals and included the material required for field aging plus storage containers and formalin for the teeth. Approximately 22 hours were required to collect, process and age 100 incisors. The field age determination method required 8 hours per 100 animals. The cementum-annulation count method also required chemicals and microscopic slides costing $16.00 per 100 incisors. Assuming an hourly wage of $4.50, the cost of labor and material would be $1.00 per animal aged by the cementum-annulation count as compared to $0.37 per animal for field aging by eruption-replacement and wear. However, the projected cost of the cementum-annulation count process was considerably below the $1.60 per tooth figure listed by a commercial laboratory. The above cost did not include microscopes, cryostat, slide warmer, staining tray or glassware. Any agency processing over 1000 teeth per year should acquire the necessary equipment.

Age determination is not the final result but furnishes a data base for population analysis.

Population Analysis

Introduction

Developing a really sound, sustained-yield harvest policy will ultimately require a thorough understanding of the population dynamics of Utah deer herds. A knowledge of age-specific reproductive and survival rates, and the effects of various environmental variables, including different levels of hunting kill will permit an insightful understanding of the role that hunting kill plays in the overall population patterns. That understanding would then provide a firm basis on which to propose annual hunting regulations.

Such an understanding for the herds of the major biotic regions of Utah, if not for each of the herd units themselves, will only come through an extensive research effort. The present study was undertaken, and is herewith reported, primarily as a pilot effort to establish and demonstrate procedures for estimating herd survival rates and population trends -- a small subset of the overall understanding advocated above. These procedures include, sequentially: (1) survival-rate calculations for the five, selected herds by the method of Robson and Chapman (1961), and (2) combining these rates with recruitment rates reported by UDWR to (3) estimate population trends from these parameters by the method of Henny et al. (1970). Calculated herd trends will then be correlated with several demographic and environmental variables to attempt to discern some of the causal factors.

Application of the Robson-Chapman and Henny et al. methods requires certain assumptions which cannot be met in the case of the five herds. The methods also call for certain population measurements which are not available for these herds. Hence the estimates ultimately derived will undoubtedly deviate from the true population parameters to an unknown degree. Consequently, the exercise which follows is presented more as an example of the use to which deer population data can be put in relating demographic patterns to harvest policies than as an attempt to derive entirely valid estimates of population parameters.

Survival rates of yearling and older does

Herd Unit 2 as an example. Age distribution of the five herds, based on cementum-annulation counts of 736 animals taken during the 1972 hunting season, are shown in Table 3. The female age distribution for the Cache Herd Unit (No. 2) will be used for calculating survival rates by the Robson and Chapman procedure, and to demonstrate the method by which survival rates for the other units were calculated.

Two conditions must hold in order to derive valid survival-rate estimates with the Robson-Chapman method. The first is that, as is the case of all methods for estimating survival rates from the age composi-

Table 3. Age distribution of hunter-killed deer (fawns excluded) from the five units.

Age (years)	Unit 1				Unit 2				Unit 23B				Unit 30A				Unit 48			
	Female		Male		Female		Male		Female		Male		Female		Male		Female		Male	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
1.5	4	10	15	16	23	21	79	56	6	15	36	43	24	45	15	41	22	27	19	37
2.5	19	46	43	46	31	29	29	20	14	36	29	35	16	19	13	35	29	35	20	38
3.5	8	20	22	24	28	26	19	13	6	15	13	16	9	17	2	5	16	19	8	15
4.5	6	15	3	3	9	8	9	6	7	18	3	4	7	13	6	16	14	17	2	4
5.5	3	7	6	6	6	6	5	4	3	8	2	2	2	4	1	3	1	1	3	6
6.5	-	-	2	2	4	4	1	1	3	8	-	-	1	2	-	-	-	-	-	-
7.5	1	2	-	-	3	3	-	-	-	-	-	-	-	-	-	-	1	1	-	-
8.5	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10.5	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-

tion of a time-specific sample of a population, is that the population in question must be numerically constant, i.e. not undergoing long-term increases or decreases (vide Seber 1973). This may not be the case with the five units under study here. Results of browse-utilization studies and pellet-group transects suggest a population decrease. UDWR personnel (John et al. 1973) stated: "... range data seems to indicate that this herd is down somewhat ..." for Unit 1 and "... deer numbers are definitely down ..." for Unit 2. Tabulation of kill estimates and hunting-success rates during the 5-year period (1968-1972) for the five units (Table 4) does not provide any conclusive evidence as to herd trend except perhaps for Unit 23B. Doe kill and hunting success generally declined in this unit from 1968 to 1971 during a period with constant hunting regulations. However, in contrast to the other herd units, the estimated number of hunters on 23B also declined substantially and may thus be partially responsible for the observed decrease in harvest. There is, nonetheless, a strong subjective impression among UDWR personnel and the hunting public that herds have been declining for several years over the state as a whole.

In a population with an annual survival rate of 0.40, an annual birthrate of 2 young produced per female of age 1 year and older, it can be shown that the survival rate implied by the age distribution at a point in time would be 0.50 (Wagner 1975). In a population with the same assumptions except a 0.60 survival rate, the implied rate would be 0.50. In the above hypothetical examples the rates of change in population size are -0.2 and +0.2 respectively. In other words, survival rates calculated from age distributions tend to overestimate the true population values in declining populations, and underestimate them in increasing populations.

Table 4. Deer herd hunting season and harvest summary.[a]

	Days total	Buck only	Either sex	Number of hunters	Buck kill	Doe kill	Total kill	Percent success
				Box Elder Unit 1				
1968	11	*	11	2,396	830	287	1,117	47
1969	11		11	3,060	958	642	1,600	52
1970	11		11	4,138	1,575	846	2,421	58
1971	11	8	3	3,835	1,313	530	1,843	48
1972	11	8	3	4,460	1,597	539	2,136	48
*1-A buck only								
				Cache Unit 2				
1968	11		11	8,799	2,357	1,825	4,182	43
1969		11	12*	8,306	2,020	1,379	3,399	41
1970	21		21	9,409	2,573	2,024	4,597	49
1971	11		11	7,269	1,665	995	2,660	37
1972	11		11**	8,458	2,071	980	3,051	36
* 2-A 11-day buck only - 12 day either sex								
**2-B 3-day either sex - 8 day buck only								
				Currant Creek Unit 23B				
1968	11		11	9,179	2,991	1,731	4,722	51
1969	11		11	7,575	1,899	1,621	3,520	46
1970	11		11	7,951	2,348	1,313	3,661	46
1971	11		11	6,812	1,883	975	2,858	42
1972	11	8	3	6,839	2,283	936	3,219	47

Table 4. Continued

	Days total	Buck only	Either sex	Number of hunters	Buck kill	Doe kill	Total kill	Percent success
				LaSal Mountain Unit 30A				
1968*	11		11	3,770	2,008	789	2,797	74
1969	11		11	3,467	1,531	738	2,269	65
1970	16		16	3,877	1,808	881	2,689	69
1971	11		11	4,026	1,399	996	2,395	60
1972	11		11	4,229	1,729	782	2,511	59
*LaSal Dolores and LaSal Mountain combined								
				Monroe Mountain Unit 48				
1968	11		11	3,186	1,639	707	2,346	74
1969	11		11	3,422	1,530	626	2,156	63
1970	11		11	4,093	1,637	980	2,617	64
1971	11*		11*	4,768	2,034	996	3,030	64
1972	11**		11**	5,507	1,927	1,410	3,337	61

* North part - 23 days
**North part - 16 days

[a]UDWR date (John 1973)

Given an independent estimate of the rate of population change, the actual survival rate may be obtained by:

$$\hat{s} = s\ (1-u) \qquad (1)$$

where $\hat{s}$ is the actual survival rate, s is the implied rate, and u is the rate of population change (Charles Fowler 1975, Personal Communication). Unfortunately, independently derived rates of population change for the five herd units in question do not exist. Hence, there is some probability that the survival-rate estimates presented below overestimate the true parameters.

A second condition which must obtain in using the Chapman-Robson technique is that the age distribution of the population segment from which the average annual survival rate is calculated is geometric or exponential. Stated differently, this assumption requires that the age-specific survival rates be equal. The assumption can be tested statistically in one of two ways by means of the chi-square statistic. However, a provisional survival rate must be calculated before either test can be applied.

Robson and Chapman's method for estimating the annual survival rate requires that age distribution be coded starting with the minimum age of the assumed geometric age distribution as shown below for Unit 2.

Age	x Coded age	Nx Number in sample
1.5	0	N_0 = 23
2.5	1	N_1 = 31
3.5	2	N_2 = 28
4.5	3	N_3 = 9
5.5	4	N_4 = 6

Age	x Coded age	Nx Number in sample
6.5	5	$N_5 = 4$
7.5	6	$N_6 = 3$
8.5	7	$N_7 = 2$
9.5	8	$N_8 = 0$
10.5	9	$N_9 = 1$

The Robson and Chapman equation for estimating survival rate(s) is:

$$s = \frac{T}{n + T - 1} \qquad (2)$$

where n is the total number in sample (107) and T represents the total number of years lived by all individuals in the segment in which the survival rate is assumed constant. Thus:

$$T = N_1 + 2N_2 + 3N_3 \ldots\ldots\ldots\ldots\ldots xN_x \qquad (3)$$

Therefore $s = \frac{199}{107 + 199 - 1} = 0.65$ or the survival rate for yearling and older does on the Cache Unit.

Chapman and Robson's (1960) equation for the variance of the estimate is:

$$V_{(s)} = \frac{T}{n + T - 1}\left(\frac{T}{n + T - 1} - \frac{T - 1}{n + T - 1}\right) = 0.0007 \text{ for the} \qquad (4)$$

Cache does and the standard error is:

$$\text{s.e.} = \sqrt{V_{(s)}} = 0.0273 \text{ for the Cache does.} \qquad (5)$$

The approximate 95 percent confidence limits are ± 2 standard errors. Thus the confidence intervals of the survival estimate are:

$$s = 0.60 \leq 0.65 \leq 0.70 \qquad (6)$$

However, since the age structure is not a continuous series, the survival rate may be calculated by combining the 10.5 year-olds with the 8.5 year-olds. Thus:

Age	Coded age	Number in sample
1.5	0	$N_0 = 23$
2.5	1	$N_1 = 31$
3.5	2	$N_2 = 28$
4.5	3	$N_3 = 9$
5.5	4	$N_4 = 6$
6.5	5	$N_5 = 4$
7.5	6	$N_6 = 3$
8.5+	7	$N_7 = 3$

The survival rate may be estimated by:

$$s = \frac{T}{n - m + T} \tag{7}$$

where m = the sample size of the combined age classes. The variance of the estimate is:

$$V = \frac{s(1 - s)^2}{n(1 - s^k)} \tag{8}$$

where k = the coded age of the combined age classes. The survival estimate is:

$s = 0.65 \pm 0.06.$

Age classes were combined when a discontinuity existed in the age structure.

An approximate test of compatability of the first age class with the remainder of the data is given by Eberhardt's (1969) formulation:

$$(Q) = \frac{(s - s')^2}{\frac{T(T - 1)(n - 1)}{n(n + T - 1)^2 (n + T - 2)}} \tag{9}$$

where $s' = \frac{n - N_0}{n}$ (10)

therefore Q = 12.73

Q is a chi-square variate with one degree of freedom, so the critical chi-square value due to chance at the 0.05 level of precision is 3.84. This does not prove survival for the yearlings in this sample different from that for the older animals but only demonstrates the lack of agreement with the assumption of geometric age distribution for the sample.

The procedure (equations 7-10) is repeated with the 2.5 year-old age class as the initial class in the coded sample. The results thus obtained are $s = 0.52 \leq 0.58 \leq 0.64$ and the 2.5 year-old class is determined to be compatible with the older age classes ($\chi^2 = 1.88$).

The second test is a comparison of the observed age distribution with a hypothetical geometric distribution, given the preliminary survival-rate estimate and the total number of deer in the sample:

$$f_{(x)} = (1 - s)s^x \tag{11}$$

where x is the coded age class. Multiplying the relative frequency $[f_{(x)}]$ by the total sample size for the segment from which the survival rate is calculated gives the expected number for each age class. The chi-square test may then be used to test the null hypothesis that the observed age distribution does not differ from the hypothetical one. Results of this test ($\chi^2 = 4.6$) also lead to the conclusion that the observed age distribution for Unit 2 is not statistically different from that expected from a geometric distribution.

The major source of the incompatibility appears to be the small number of yearlings in the sample, a characteristic of four of the doe collections and at least three of the buck samples (Table 3). Since the yearlings were aged by tooth eruption at checking stations they, among all the adults, were aged most nearly without error. Hence, it seems possible that a technician, working at a checking station and collecting jaws for annulation aging, might assume that only those which could not be aged unequivocally were desired. He might then choose not to remove some yearling jaws during peak rush periods at the station, and only remove them at times when the pressure was not heavy. Many of the 517 incisors collected to increase sample size for population analysis were collected during slack periods.

This suspicion can be explored by recourse to UDWR aging data (John et al. 1973) for these same units. Percentages of yearlings recorded through field aging of all the does checked during the 1972 season at the stations for Units 1, 2, 23B and 30A (data not available for Unit 48) were 10, 23, 30, and 37 percent respectively. These compared with 10, 21, 15 and 45 percent in the annulation samples used in this study (Table 3). The results of this comparison are inconclusive since both sets of data were collected simultaneously.

The second approach is to compare incidence of yearlings in 1972 with that in previous years. UDWR data indicate that the 1967-1971 average percentage of yearlings for the period 1967-1971 were 35, 45 and 41 percent for Units, 1, 2 and 23B respectively and 41 percent on Unit 30A during 1970-71 (vide John et al. 1973). When these higher values are substituted for the lower yearling numbers in Table 3, the series become geometric through the yearling class by Eberhardt's (1969) test.

Several authors have addressed the question of possible differential yearling vulnerability to the gun, but the findings are somewhat ambiguous. Maguire and Severinghaus (1954) presented evidence to show that yearling white-tailed deer in New York are more vulnerable to hunting than older deer. Eberhardt (1960) questioned the methods used by these authors, but after analysis of Michigan data, concurred with their general conclusion that yearlings are slightly more vulnerable than older deer. More recently Severinghaus (1969) considered the age distribution for both sexes among yearling and adult deer representative of the actual population composition. He did note, however, that the proportion of yearlings (especially females) was abnormally low in some years. Smith et al. (1969) demonstrated a greater vulnerability of yearling bucks to hunting among Arizona mule deer, but found no discrepancy in harvest rates between yearling and adult does. Finally, Taber and Dasman (1957) presented survivorship curves from other deer herds (e.g. Danish roe deer. *Capreolus capreolus*; and California black-tailed deer, *O.h. columbianus*, which visually appear to be geometric through the yearling age class. Similar evidence has been given by Hoekstra (1971) and Mech and Frenzel (1971) for hunter-killed deer in southern Indiana and northeastern Minnesota, respectively.

The higher average percentage in the 1967-71 field-aged collections, plus the lack of consistent evidence suggesting lower vulnerability of yearling does in other deer herds, would seem to lend support to the suspicion that yearlings were undersampled. For the purpose of this exercise I conclude that the age distributions of adult does characteristically approach the geometric or exponential, that the survival rate can be calculated on that portion of the sample which includes the 2.5-year and older deer, and that the resulting survival rate can be extrapolated to the 1.5-2.5 year interval. Accordingly the corrected number of yearlings in Table 3 distributions can be calculated with these survival rates and the year classes shown in the table.

Recalculation of the Unit 2 doe survival rate on the basis of the 2.5 and older animals now yields a value of 0.58 ± 0.07. The adjusted yearling sample becomes 60 on the basis of Equation 11.

Survival rates for the other four units. The same procedures described above were applied to the doe samples from the other four units: (1) test for geometric distribution; (2) calculation of adult doe survival rate on the basis of 2.5 year-olds and older animals; and (3) recalculation of yearling age class. The results are summarized in Table 5.

Table 5. Geometric age distributions and survival rates of adult does

	Unit				
	1	2	23B	30A	48
Chi-square test of geometric fit: $f_{(x)} = (1-s)s^x$ [a]	1.3	4.6	3.7	1.8	8.1
Yearlings compatible with older does [a,b]	No	No	No	Yes	No
Adult doe survival rate and 95 percent confidence limits [c]	.58±.11	.58±.07	.58±.11	.58±.04	.46±.10
Adjusted yearling component in Table 4	27	61	26	25	72

[a]Based on doe distribution in Table 4
[b]Eberhardt's (1969) compatibility test
[c]Based on 2.5-year old and older does in Table 4

First-year female survival rates

Estimates of first-year survival rates (s_0) are essential for the Henney et al. (1970) method of determining population trend. Since there is evidence that fawns are more vulnerable to the gun than older age classes (Hayne and Eberhardt 1952), but that hunters also prefer to shoot older and larger animals, the fawn samples are subject to opposing biases of unknown magnitude. Hence, they were not included in the age distributions shown in Table 3, nor used for calculating first-year survival rates.

Instead, the following change-of-ratio approach was used (Hansen 1963). UDWR personnel annually conduct prehunting-season (late summer and early fall) herd composition counts from which fawn-doe ratios are estimated. The does observed include yearling females which were not of breeding age roughly 13-14 months previous when the fawns now being observed were conceived. Hence, the observations include fawns roughly 3 months of age, yearlings, and the 2.5-year old and older does which produced the fawns.

If we can assume that the hunting-season age distributions accurately reflect the population age distributions, then the ratio of yearling does to 2.5 year-old and older does can be applied to the preseason composition data. This provides an estimate of the proportion of yearlings and of breeding does in these observations, and ultimately permits an estimate of the number of fawns per breeding doe in the population at this time of the year. Since the fawns of a given year become the yearlings of the next, their survival rate from autumn (or late summer) as fawns to the following autumn as yearlings can be calculated by the following relationship:

$$\text{1st yr. doe survival rate} = \frac{\text{Yrlg. does/adult doe in yr. n+1}}{\text{Doe fawns/adult doe in yr. n}} \qquad (12)$$

Assuming a fawn sex ratio of 50:50, the number of female fawns in the observations can be obtained by halving the total fawns observed in herd composition surveys.

This method provides valid estimates only if the preseason observations and hunting-season data are unbiased observations of population age composition, and if the population is stable. If the population is declining, the survival rate will be overestimated. The converse would be true of a growing population.

In order to make these estimates for the five herd units under study here, UDWR preseason observations on the units over the period 1968-72 (John et al. 1973) were used for the fawn-doe ratios (Table 6).

Table 6. Calculation of first-year female survival rates

	Unit				
	1	2	23B	30A	48
Average preseason fawns/ 100 does (1968-72), 95 percent confidence limits and sample sizes (in parentheses)	79±16 (519)	78±13 (1427)	96±14 (534)	86±9 (1322)	80±8 (923)
Percent of adult does that are yearlings (1.5 years old)[a]	10	23	30	37	--[b]
Calculated first-year survival rate[c]	0.62	0.01	0.71	0.92	--

[a]Based on UDWR field-aging data during 1972 season (John et al. 1973)
[b]Data not available
[c]From Equation 12

Since the yearling percentages observed in this study (Table 3) were not compatible with the geometric distributions of the 2.5 year-old older animals in four of the five units, the checking-station yearling percentages derived by UDWR personnel during the 1972 hunting season were used for Units 1, 2, and 23B (Table 6). The proportion of yearlings obtained in this study was compatible with the geometric distribution of the remaining year classes for Unit 30A; it was used for the first-year survival calculation.

The resulting first-year survival estimates (Table 6) agree in two cases (Units 1 and 23B) with the range reported by Robinette (1956) for Utah mule deer (60-80 percent). In two cases (Units 2 and 30A), however, the estimates were evidently too high. On the possibility that the small samples produced the variation, a statewide first-year survival rate was calculated from data on 22 units. This included all units from which the preseason composition counts and the age and classification of the harvest were available. This produced a statewide average first-year survival rate (s_0) estimate of 0.72 with a standard deviation of 0.02. This compares favorably with the figures given by Robinette (1956).

Recruitment rates

A final estimate needed to calculate population trend is that of the annual recruitment rate ($2\overline{m}$) per breeding doe (2.5 + years old) as calculated by Henny et al. (1970):

$$2\overline{m} = \frac{\overline{x} \text{ fawns/100 does}}{\text{adult doe survival rate} \times 100} \qquad (13)$$

where the fawn-doe statistics are given in Table 6, and female survival rates are shown in Table 5. The result is the number of fawns per doe during the preseason trend count.

For the Cache Herd Unit this estimate is:

$$2\overline{m} = \frac{78}{0.58 \times 100} = 1.34 \text{ fawns per breeding doe}$$

The values for the other four units by this same method are: Unit 1, 1.36; Unit 23B, 1.72; Unit 30A, 1.50; Unit 48, 1.74.

Population trends

Calculation of trends. Henny et al. (1970) and Henny (1972) provided equations and tabulated rates by which population rates of change could be determined, given values for recruitment, s_0 and s_1. I have modified two of their tables for use here (Tables 7 and 8). These tables show the recruitment rates needed to maintain populations with different first-year and adult survival rates.

The Cache herd, with a first-year doe survival rate (s_0) of 0.72 and an adult doe survival rate of 0.58, would require a recruitment rate of 1.91 fawns per breeding (2.5 + years) doe to maintain its population level (Table 7).

The general population model proposed by Henny et al. (1970) is written as:

$$1 = m_1 s_0 (1+u)^{-1} + m_2 s_0 s_1 (1+u)^{-2} + m_3 s_0 s_1 (1+u)^{-3} + \ldots \quad (14)$$

where m_x = age-specific recruitment rate of young per breeding doe

s_x = age specific survival rate

u = annual rate of change in population size

The equation is similar to Lotka's (1939) Equation 32 except that Lotka's equation assumed constant birth rate with age. When the adult doe survival and recruitment rates are constant with age and all does breed at 2 years of age, the above equation reduces to (Henny et al. 1972):

$$(1+u)\ (1+u-s_1) = (m s_0 s_1)$$

where s_0 = first-year survival rate

s_1 = adult survival rate

m = average doe-fawn recruitment per breeding doe

Table 7. Recruitment rate per breeding doe (2.5 + years old) for a stable population. The tabulated values represent fawns of both sexes per breeding doe.

		First-year doe survival rate (s_0)								
		50%	55%	60%	65%	70%	75%	80%	85%	90%
	45%	4.89	4.48	4.07	3.78	3.49	3.27	3.05	2.89	2.72
Adult	50%	4.00	3.67	3.34	3.10	2.86	2.68	2.50	2.36	2.22
female	55%	3.27	2.98	2.73	2.51	2.34	2.19	2.04	1.93	1.82
survival	60%	2.67	2.42	2.22	2.06	1.91	1.78	1.67	1.58	1.48
rate	65%	1.71	1.56	1.43	1.32	1.22	1.14	1.07	1.01	0.95
(s_1)	70%	1.33	1.21	1.11	1.03	0.95	0.89	0.84	0.79	0.74
	75%	1.00	0.91	0.83	0.77	0.71	0.67	0.63	0.59	0.55
	80%	0.80	0.73	0.67	0.62	0.57	0.53	0.50	0.48	0.45

Table 8. Recruitment rate per adult doe (1.5 + years old) required for a stable population. The tabulated values represent fawns of both sexes per adult doe as observed during preseason trend counts.

		First-year doe survival rate (s_0)								
		50%	55%	60%	65%	70%	75%	80%	85%	90%
	45%	2.20	2.02	1.84	1.71	1.57	1.48	1.38	1.30	1.22
Adult	50%	2.00	1.84	1.67	1.55	1.43	1.34	1.25	1.18	1.11
female	55%	1.80	1.63	1.50	1.39	1.28	1.21	1.13	1.06	1.00
survival	60%	1.60	1.45	1.38	1.24	1.15	1.07	1.00	0.95	0.89
rate	65%	1.40	1.27	1.17	1.08	1.00	0.94	0.88	0.83	0.78
(s_1)	70%	1.20	1.09	1.00	0.92	0.86	0.80	0.75	0.71	0.67
	75%	1.00	0.91	0.83	0.77	0.71	0.67	0.63	0.59	0.56
	80%	0.80	0.73	0.67	0.62	0.57	0.53	0.50	0.48	0.45

Substituting values of previously derived parameters in Equation 15 and solving for u, we can estimate average annual rate of population change for the Cache deer herd at -12 percent for the period 1968-72. Rates of population change calculated by the same method for the other units were: Unit 1, -11 percent; Unit 23B, -7 percent; Unit 30A, -8 percent; Unit 48, -20 percent. The calculated herd trends, as derived from uncertain data available, are all negative. This is also the general consensus of UDWR personnel, as well as the hunting public.

Factors Affecting Herd Trends

The Henny et al. (1970) equation for determining the rate of population change contains two variables: adult female survival rate and productivity. The importance of the first parameter is illustrated by the following example. If we assume that $2\overline{m} = 1.6$, $s_0 = 0.6$, and $s_1 = 0.5$, then u can be calculated as follows:

$$(u+1)\ (u+1 - 0.5) = (0.8)\ (0.6)\ (0.5)$$

$$u = -0.20$$

Now changing s_1 to 0.6, we obtain:

$$(u+1)\ (u+1 - 0.6) = (0.8)\ (0.6)\ (0.6)$$

$$u = 0.085$$

In other words, increasing the adult female survival rate by 20 percent results in a 58 percent decrease in the rate of population change. To obtain an equivalent degree of change in this parameter, it would be necessary to increase the recruitment rate ($2\overline{m}$) proportionately (i.e. to 2.54).

The importance of the adult female survival rate as a determinant of herd trend is also illustrated by the results of correlation-regression tests. The correlation (r^2 = 0.72) between the adult doe survival rate and the population rate of change was significant at the 0.10-level but not at the 0.05-level of probability. Productivity versus the rate of population change (r^2 = 0.38) was not significant.

The index of hunting pressure (Table 9) was the major determinant (r^2 = 0.88; see Fig. 6) of the rate of population change. This correlation was significant at the 0.05-level of probability. The correlation between hunting pressure and adult female survival was fairly high (r^2 = 0.59) but not significant.

Other correlation-regression tests included: productivity versus the population's rate of change, ratio of winter to summer range areas versus population's rate of change, productivity versus the ratio of winter to summer range areas. The correlations for these tests were not significant.

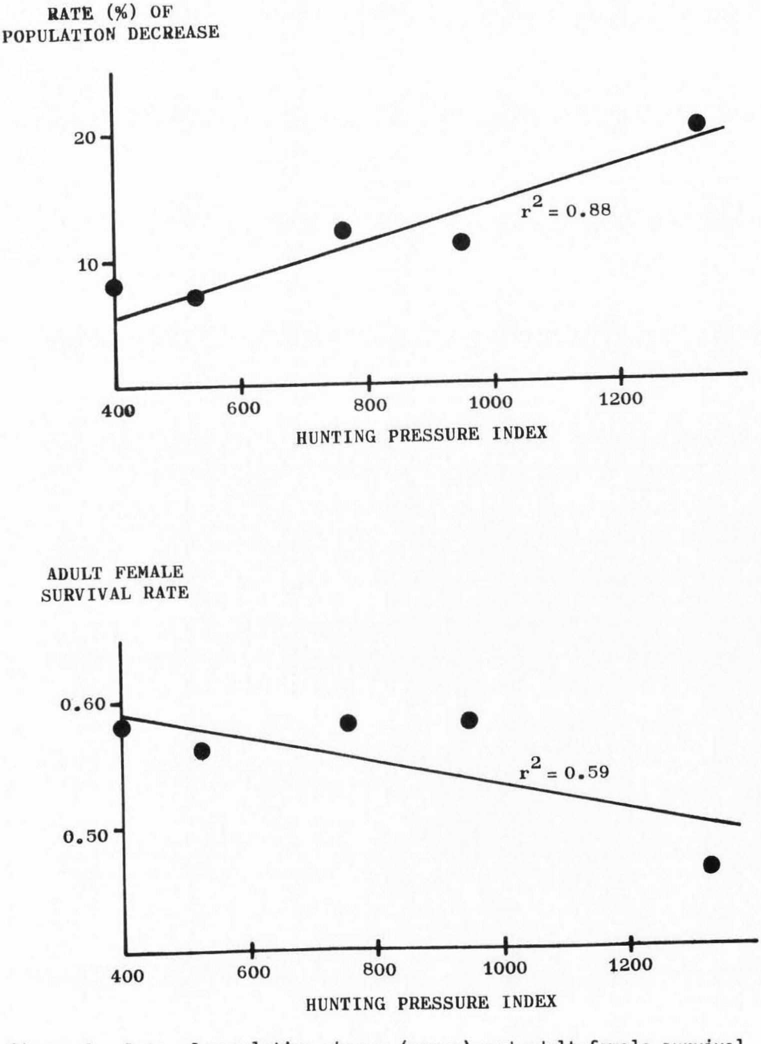


Figure 6. Rate of population change (upper) and adult female survival rate (lower) as a function of an index of hunting pressure. See text for derivation of the hunting pressure index.

Table 9. Derivation of the hunting pressure index

Unit	Hunters[a]	Days hunted[b]	Summer range area (km^2)[c]	Hunter days/(km^2)	Days of either sex season[d]	Hunting pressure index[e]
1	3578	2.7	394	24.9	38	946
2	3448	3.1	1880	14.1	54	762
23B	7671	3.1	2110	11.2	47	526
30A	3874	3.6	2120	6.6	60	397
48	4195	3.5	700	20.7	64	1327

[a] 1968-72 average from Table 5
[b] From UDWR data (John 1973)
[c] From Table 1
[d] Summation of values in Table 5
[e] Hunter days/km^2 x days of either sex season

SUMMARY AND RECOMMENDATIONS

Although preliminary in nature, this project demonstrates procedures for estimating herd survival rates and population trends. These procedures include: (1) survival rate calculations for each herd by the methods of Robson and Chapman (1961); and (2) combining these rates with the recruitment rates observed during preseason herd composition counts to (3) estimate population trends from these parameters by the methods of Henny et al. (1970). The high correlation values between the population trend and the hunting pressure index are indicative of a means for quantifying both hunter pressure and herd impact.

UDWR personnel determined deer ages to one of five age classes, i.e., fawn, yearling, 2.5-year old, prime, and old. Calculation of survival rates was not practical with these data. Hence, the tooth eruption-replacement-wear method and the cementum-annulation count techniques were compared. The cementum-annulation counts not only proved to be accurate as a means of age determination, but also provided ages that were determined to specific year classes not merely wear class.

With the ages determined to year classes, survival rates were calculated by methods of Robson and Chapman (1961). Upon analysis of the survival rates and the age structures, several disturbing factors became apparent. Eberhardt's (1960) compatibility test revealed that the yearlings were not compatible with the older segment of the age structure. The chi-square test which was used to test the hypothesis that the age distributions were geometric also disclosed a shortage of yearlings in the samples. A comparison of the ratio between yearlings and 2.5 + year-olds in my sample versus UDWR (1973) data for 1967-71 indicated that the yearlings were not adequately sampled.

Another possible source of bias is that the incisors were collected from the first 40-60 percent of the deer harvested. Indications from UDWR personnel are that this would be a bias towards the younger age classes and, therefore, an underestimation of survival rates.

The first-year survival rates, as calculated by change-in-ratios, are fraught with bias. Again the major one is the dynamics of the population. Also the data furnished by UDWR may contain bias on the visibility and distribution of does with fawns versus does without fawns during the preseason trend counts and during the hunting season. If such biases exist, they may be constant from year to year, yielding reliable trend data, but not the actual first-year survival rate. Bias in the adult doe age distribution will also bias the first-year survival rate. The first-year survival rate calculated above is at best only a crude estimate.

A major source of variation was the small sample sizes involved in the estimation of the adult female survival rate. This raises the question of the sample size required to obtain reliable estimates of survival rates. When the age distribution is geometric and survival rate is 0.55 (the mean of the five survival rates from Table 5) a sample of 175 incisors would be required to obtain a 0.05 level of precision. The variances and confidence intervals of the survival rate (55 percent) at the various sample sizes are tabulated below:

sample	=	25	then the	=	0.0045	95 percent	=	±0.134
size		50	variance		0.0022	confidence		±0.094
		75	of the		0.0015	interval of		±0.078
		100	survival		0.0011	the survival		±0.066
		125	rate		0.0008	rate		±0.059
		150			0.0007			±0.054
		175			0.00064			±0.050
		200			0.00060			±0.048
		250			0.00045			±0.042
		500			0.00022			±0.030

A higher survival rate would require a larger sample size. For most Utah deer herds a sample size of 200 doe incisors would be adequate for determination of the survival rate estimates and the age distribution at a 0.05 level of precision.

The qualifications of herd impact by hunter pressure indicates the possibility of developing a formula with which UDWR could prescribe seasons or regulations to get a specific harvest which would allow herd increase, herd stability at a desired density or a particular rate of reduction. This would be accomplished by adjusting the hunting pressure on the doe population by some combination of either-sex hunting days or a limited number of either-sex hunting permits. Under the conditions existing during the fall of 1972 a complete closure of doe seasons would have established the populations at the preseason levels. All of this emphasizes the value of population analysis, and it stresses the importance of working out the biases in, and narrowing the confidence intervals for, the data used in the population analysis.

The objective of most deer management programs is to maintain the largest huntable population which the habitat can maintain in a healthy condition. Attainment of this objective falls into two major categories: the manipulation of habitats to make them suitable for maintenance of deer and, secondly, the management of populations to keep them at equilibrium with their habitat and compatible with other land uses. The management ideal is to understand what the effects of different herd levels are on vegetation, then select the level which maintains the vegetation at a maximum primary production for deer utilization on an equilibrium basis, thus maintaining that herd level through sustained-yield harvest patterns. Hence, it is just as important to understand the ecology of the vegetation and how it responds to browsing as it is to understand the deer population dynamics and how they respond to exploitation.

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