

AN ABSTRACT OF THE THESIS OF

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Title: Population Ecology of the Columbian White-tailed Deer.

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E. Charles Meslow

A population of Columbian white-tailed deer (CWTD) was studied on a refuge (790 ha) in southwestern Washington during 1972-77. Quality of habitat was considered good for these deer and total population size remained between 164-230 as determined by mark-recapture methods during November. Population size declined significantly between the winters of 1974-75 and 1975-76. All sex-age classes exhibited a contagious dispersion on the study area; the locations of high density areas among these classes differed slightly. Sex ratio at birth did not differ significantly from 1:1, but females outnumbered males 3:1 among yearlings and adults. Fawn:doe ratios ranged from 35-60 fawns per 100 does in November. From 1972-77, yearling and adult males comprised 18-21% of the November population, yearling and adult females 50-60% and fawns 21-31%. Limited data on reproduction indicated that all yearling and adult females bred and typically carried 2 fawns, while female fawns did not breed. There was a significant inverse correlation between recruitment rates of marked females (≥ 3.5 years old) and the population estimate for November of the previous year ($r = -0.999$, $P < 0.05$). Winter mortality of yearling and adult males was significantly higher than expected and 77% of all fawn carcasses located were estimated to have died during summer. In 1975-76, female mortality was concentrated in a central portion of the study area where habitat quality had presumably declined. Median ecological longevity was 2.97 for males and 4.87 for females; median age at death was significantly greater for females than males. This was due to the higher mortality rate for males (0.345) than for females (0.179) at least 1 year old. Proximate causes of death

included automobiles, bacterial infections, coyotes, dogs, drowning, nutritional stress and accidents. Based on the timing of mortality for males and females, stress due to breeding activities and fawning, respectively, were probably ultimate causes of death. CWTD were not migratory and exhibited remarkable sedentary tendencies. Mean home range size for females was 112.9 ha using the convex polygon method and 158.5 ha with the determinant method; for males, mean area of home ranges with each method was 137.7 ha and 192.2 ha, respectively. Home ranges tended to become smaller with increasing age among females, but larger with increasing age among males. Several marked females exhibited behavior that could be termed territoriality. Estimates of effective population size for this near-insular population ranged from 47-67, depending on which system of copulatory success we simulated for males. Although we detected no movement of deer onto the refuge, only about 1 immigrant per generation would need to breed successfully to eliminate fixation of genes due to random genetic drift. Stability of population size documented for this population could have been enforced by several negative feedback mechanisms that were suggested, but not substantiated, by the field data.

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PREFACE

The purpose of this page is to clarify the role played by numerous individuals in the initiation, direction and participation in the Columbian white-tailed deer project. Preliminary discussions regarding the feasibility of studying these deer were held between the late Howard Wight, then Leader of the Oregon Cooperative Wildlife Research Unit, and David Marshall of the U.S. Fish and Wildlife Service. The first phase of the research, however, was initiated by Dr. Paul A. Vohs, Jr. of Oregon State University and his graduate student, Lowell Suring. Suring collected all of the data during 1972-73, much of which he generously provided for my use in this thesis. Richard Vowles collected data during the summer of 1973 under direction of Dr. Vohs, who left Oregon State in June 1974 after negotiating the contract with the U.S. Fish and Wildlife Service under which my research was performed. I began my field studies in June 1974 under the supervision of Dr. E. Charles Meslow, my major professor. I am solely responsible for all data collected since that month, including its analysis, presentation and interpretation, and for the synthesis of all data sets that collectively comprise this thesis.

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POPULATION ECOLOGY OF THE COLUMBIAN WHITE-TAILED DEER

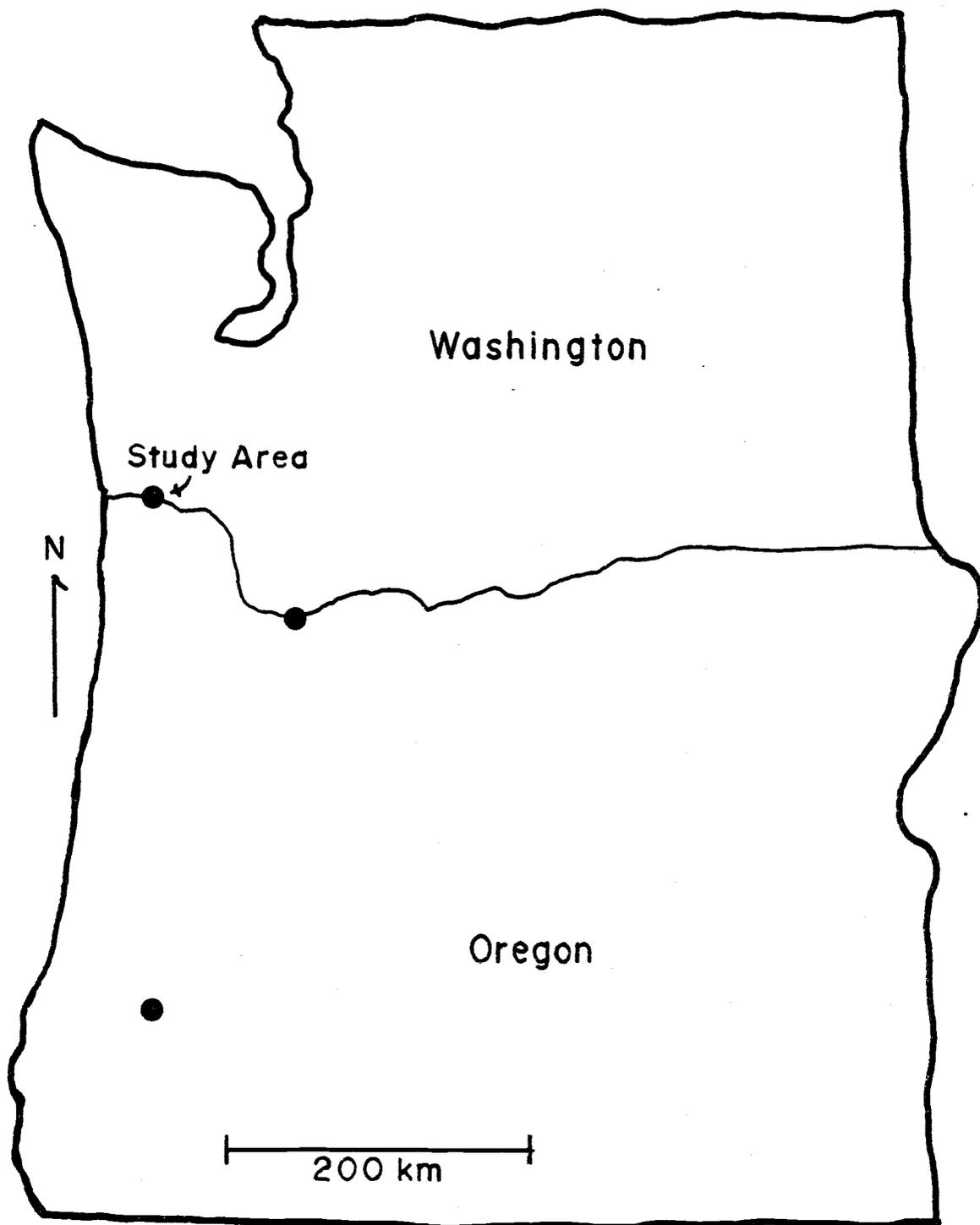
INTRODUCTION

The Columbian white-tailed deer (*Odocoileus virginianus leucurus*) has been officially listed as an endangered species by the U.S. Department of Interior since 1968. There are currently 38 recognized subspecies of *virginianus*, which contribute to a broad distribution that extends through all of the 48 contiguous states except most of Utah, Nevada and California, and from southern Canada to northern South America (Whitehead 1972). The Key Deer (*O. v. clavium*) of the Florida Keys is the only other endangered subspecies within the complex. The subspecies *ochrourus* is closest geographically to the Columbian white-tailed deer (CWTD); it is found approximately 300 km to the east of the easternmost portion of *leucurus*' present range.

The CWTD was originally described in 1829 by David Douglas, a Scottish botanist and naturalist, whose description was based on 2 specimens collected in western Oregon (Douglas 1829). He considered whitetails to be common in the river bottoms along the Cowlitz River in southwestern Washington and the Willamette River in western Oregon as far south as the Umpqua River in Douglas County (Douglas 1914). Douglas also observed whitetails along the Columbia River as did Lewis and Clark in 1806, who reported seeing them from what is now The Dalles, Oregon west to Astoria, Oregon on the coast (Thwaites 1905).

At present, there are only 3 geographic areas that contain known CWTD populations within the historic range of *leucurus* (Fig. 1). It was this limited distribution and imminent threat to whitetail habitat by agricultural and residential development that prompted its classification as endangered. In 1972 the U.S. Fish and Wildlife Service purchased 2105 ha of Columbia River shoreline and islands to establish the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR). The mainland portion of the Refuge contained the most dense population of CWTD in existence and served as the area for this study. CWTD were also found on refuge (e.g., Hunting, Price and Tenas Illahee Islands)

Figure 1. Locations of the 3 geographic areas in the Pacific Northwest where Columbian white-tailed deer are known to exist.

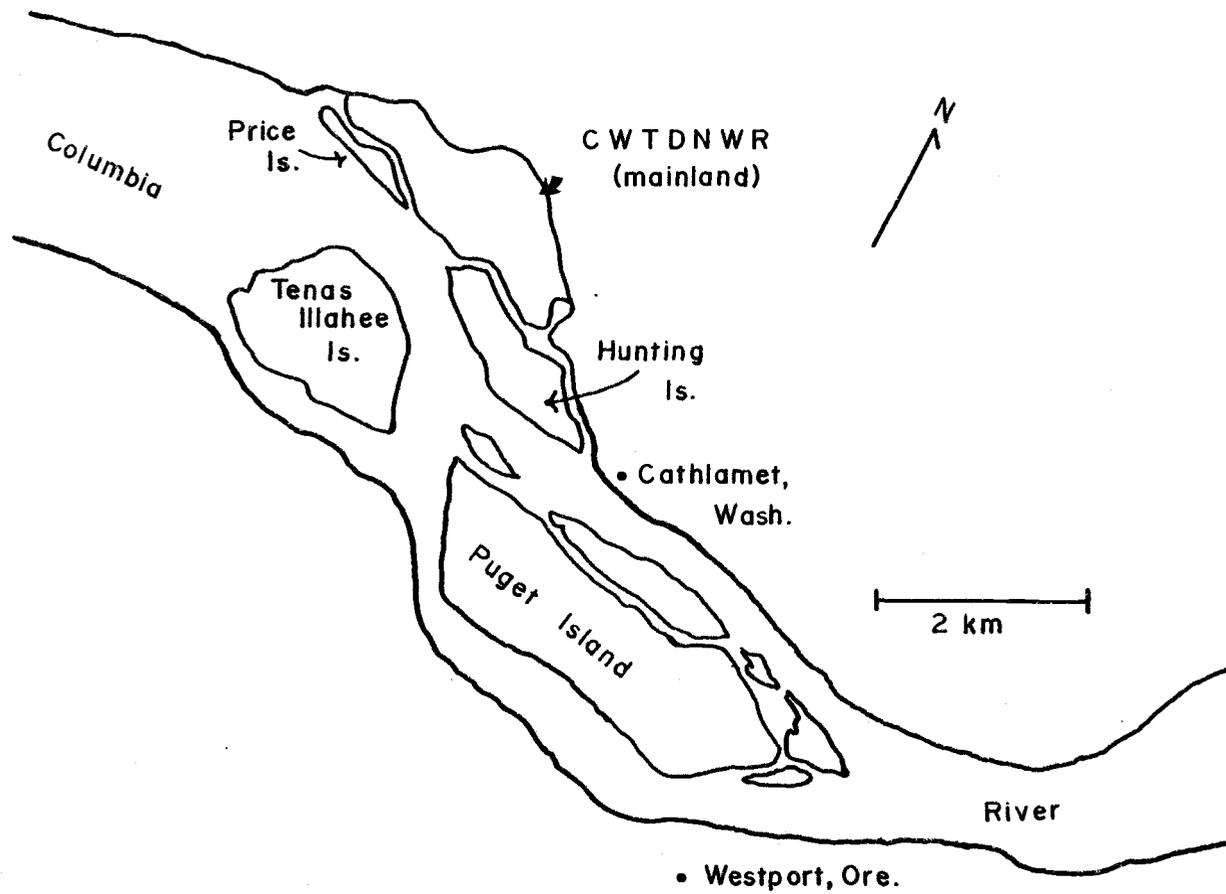


and private (e.g., Puget Island) land adjacent to the study area (Fig. 2). Whitetail densities on these islands were thought to be so low and movement between them and the Refuge mainland so limited that they probably had a negligible impact on the ecology of the study population. Gavin (1978) emphasized the importance of understanding the biogeography of all CWTD populations along the lower Columbia River, in order to appraise this taxon's status and guide management schemes.

Since establishment of the CWTDNWR, Refuge personnel have been interested in the ecological requirements of these deer, so that sound management of this "key" CWTD population could be effected. Suring and Vohs (in press) reported on habitat use by whitetails of this same population and Suring (1974) provided additional information, much of which has been incorporated with the data presented here. This paper treats data collected during a 5-year period (1972-77) on the population ecology of the Refuge herd. Our approach was to take advantage of the high visibility of this relatively dense population in order to examine birth and death processes, movements, sex and age composition, density and dispersion, and those aspects of spatial and social organization that might help to explain the population dynamics observed. The stability of this un hunted population's size throughout the 5 years of this study and the suggestion that this stability had existed since at least 1939, during which the population experienced light to moderate buck-only hunting, was the background against which our investigation proceeded. We felt that an understanding of the factors controlling the growth of this refuge population was germane to effective management of CWTD and its eventual restoration; these same factors are of general interest to students of vertebrate population ecology.

We will use the term "population" throughout this report to mean a "set of organisms belonging to the same species and occupying a clearly delimited space at the same time" (Wilson 1975). This, of course, does not imply a total absence of gene flow among such groups, so that an occasional immigrant to the Refuge mainland herd from an adjacent area, though undetected, does not negate the concept as defined above.

Figure 2. Location of the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR) mainland and nearby islands along the lower Columbia River.



THE STUDY AREA

The whitetail population of interest occurred on the 790 ha mainland portion of the CWTDNWR in southwestern Washington. The Refuge, located in Wahkiakum County between Cathlamet and Skamokawa on the north bank of the Columbia River, lay about 50 km east of the Washington coast at an elevation of 3 m above sea level. Topography was flat and Ocosta silty clay loam was the predominant soil type formed on the low, poorly drained flood plains. The natural vegetation of the area was classified as a "tideland spruce" community of the Picea sitchensis Zone by Franklin and Dyrness (1973). The Refuge mainland was part of the Columbia River flood plain and subject to tidal influences before the area was diked early in the century. Drainage of the Refuge was effected by a 60 hp pump and a series of tide gates; drainage ditches and sloughs crisscrossed the entire study area (Fig. 3).

With the water level controlled, clearing and subsequent agricultural development of the area proceeded steadily over several decades. A series of aerial photographs revealed that removal of woody vegetation was a nearly continuous process before Refuge establishment in 1972. From 1939 to 1972 the percentage of the study area in woodland decreased from approximately 66 to 17 (Table 1). As woodlots were removed, pastures were created and seeded to grasses and forbs. In 1972-73, the major plant communities on the study area and their percentage of total area were: rush (11), thistle (21), grass (43), horsetail (trace) and forest (17) (Suring and Vohs, in press). Drainage ditches and sloughs composed the remaining 8% of the Refuge mainland. Appendix A includes a list of the prominent plant species, both native and introduced, that have been identified from the study area.

Temperatures along the lower Columbia River are moderate; mean monthly maximum temperature was 17.7 C in August and mean monthly minimum was 4.0 C in January over the past 15 years during the hottest and coldest months, respectively. Although rainfall can vary significantly within a short distance in this area, mean annual rainfall near the Refuge was 270 cm, with an average of 211 cm falling from October to

Figure 3. Columbian White-tailed Deer National Wildlife Refuge mainland. (Stippled area = woodlots, diagonal lines = unit R4, dashed lines = sloughs and drainage ditches, solid lines = roads).

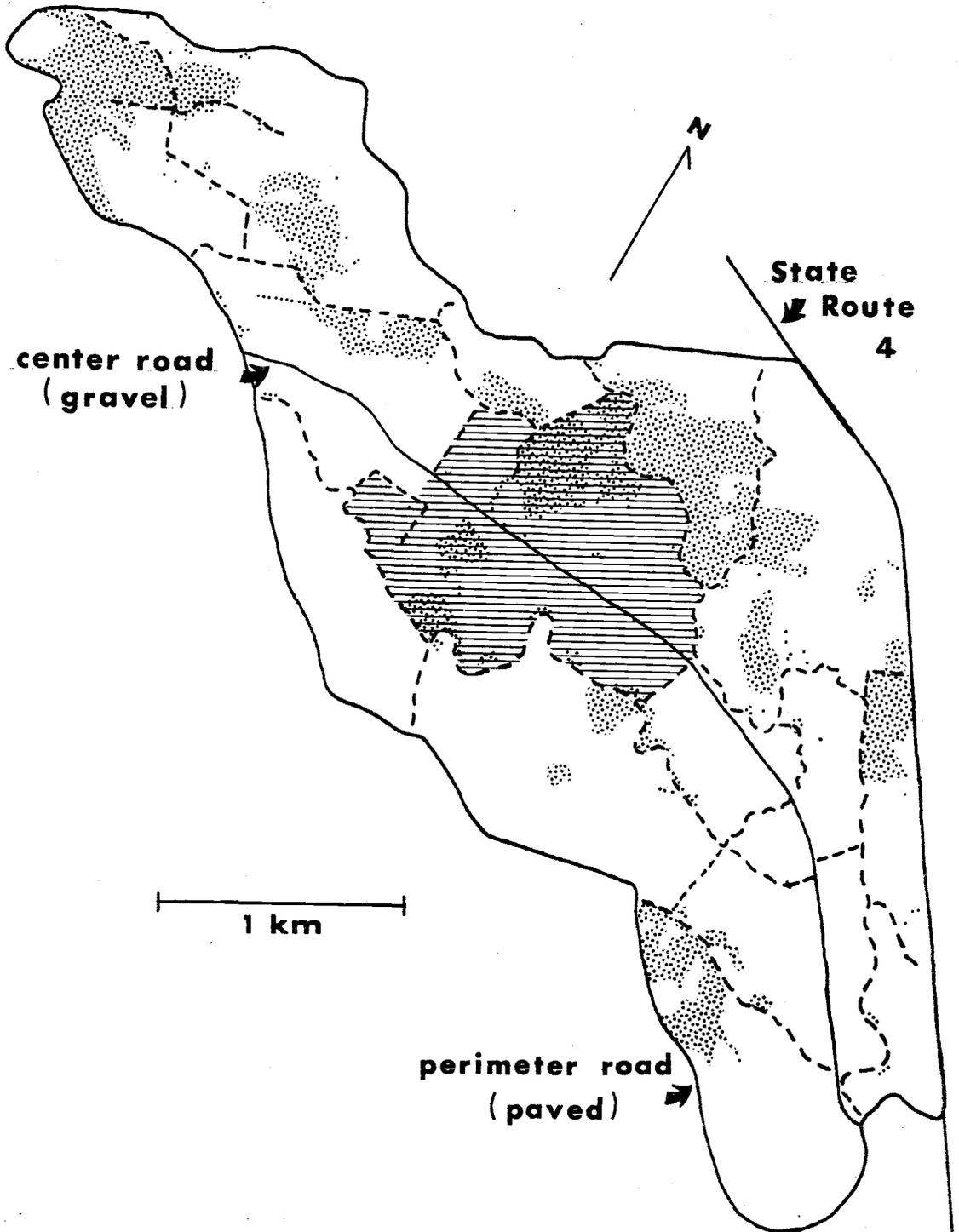


Table 1. Changes in woodland cover on the CWTD National Wildlife Refuge (Washington mainland) from 1939 to 1972, as determined from aerial photographs.

Year	Woody cover (ha) ^a	Study area in woodland cover (%)
1939	521	66
1953	347	44
1961	282	36
1965	181	23
1967	169	21
1972	131	17

^aTotal area of Washington mainland = 789 ha.

March (R. B. Webb, pers. comm.). There was seldom any snow cover on the Refuge and when it occurred persisted only 1-3 days.

The area has a history of intensive agricultural use for both dairy and beef cattle. Before 1972 the 790 ha area supported 2200-2400 head of cattle from 4-12 months of the year (Eli Doumit, pers. comm.). Approximately 400 ha received 1 cutting of hay in addition to being grazed by domestic stock. Since a high density of whitetails (1 per 2-4 ha) had been associated with this grazing regime, Refuge personnel opted to retain similar land use patterns after establishment of the Refuge in view of a paucity of ecological information about these deer. During 1973-77, a mean annual grazing intensity on the Refuge of 3743 AUMs (i.e., animal use months) was obtained by grazing an average of 41% of the study area. An average of 16% of the area was cut for hay each year, while the remaining 43% was left fallow.

The Refuge mainland is bordered by the Columbia River on the south and west and on the north and east by wooded hills typical of the Tsuga heterophylla Zone of the Coast Range (Franklin and Dyrness 1973). This boundary between flood plain and Coast Range is further enforced by the presence of a paved, 2-lane state road (Fig. 3). Black-tailed deer (Odocoileus hemionus columbianus) were common in this Coast Range coniferous habitat while whitetails were rarely observed outside the river bottomland. Thus, the Columbia River, a state highway, and habitat apparently not suitable for CWTB all served to restrict this population to an "ecological island".

Coyotes (Canis latrans) were common on the Refuge during the study and stray domestic dogs were occasionally observed. No other potential predators of deer were observed on the study area. Black-tailed deer were frequently seen, although observations probably represented repeated sightings of the same individuals; Roosevelt elk (Cervus elaphus roosevelti) were only occasionally present during 1972-76. A herd of 16-18 elk appeared on the Refuge in January 1977, but left the area prior to calving in the spring. A slightly larger herd returned in the autumn of 1977 and may have established residence.

MATERIALS AND METHODS

Field studies were conducted by Suring on a full-time basis from June 1972-June 1973 and by Gavin from June 1974-March 1976. Gavin also collected data during periods of observation of 2-5 days duration in April, May, June and November 1976 and in January, May, June and November 1977. Observations of marked deer during the summer of 1973 by R. H. Vowles were also included. We observed deer through binoculars and a 15-60X spotting scope, while on foot, in a truck, and from 2 observation towers erected about 9 m above the ground.

Statistical references were taken from Sokal and Rohlf (1969). Frequency data were analyzed using a G-test, instead of the more traditional chi-square test, as recommended by these authors (1969:560), and a probability level of less than 0.05 was considered statistically significant. Yates' continuity correction for small sample size was applied to frequency data when N was less than 50 and caution exercised in interpreting results with samples of this size. A CYBER 70 and a CDC 3300 computer aided in summarization and analysis of data.

Botanical nomenclature followed Hitchcock and Cronquist (1973).

Capture, Handling and Marking

Deer were captured by various methods from 1972-76, including the use of a 18.3 m X 12.2 m rocket net (Wildlife Materials, Inc.) and the remote injection of an immobilizing drug fired from either a Pneu-Dart rifle (Pneu-Dart, Inc.) or a Cap-Chur gun (Palmer Chemical & Equipment Co., Inc.). Tranquilizing darts were fired at deer 10-30 m away after we approached by stalking during daylight or at night with the aid of a spotlight. Projectiles used with the Pneu-Dart rifle contained succinylcholine chloride in powdered form; drugs used with the Cap-Chur darts included liquid succinylcholine chloride, a combination of etorphine hydrochloride (M .99) and xylazine, or CI-744, which was composed of tiletamine hydrochloride and zolazepam hydrochloride in equal amounts by weight (Parke, Davis and Co. 1974). Fawns less than 1 month

old were located by walking through fields and woodlots and by observing the behavior of adult does (Downing and McGinnes 1969); fawns were then captured by hand.

Once captured, we noted the deer's sex, age and general physical condition, and took a set of morphological measurements. A colored, numbered aluminum ear tag and a colored strip of "SAFLAGS" material 10-15 cm long were attached to 1 ear. Deer over 6 months old were also fitted with a white collar made of polyvinylchloride and bearing a large black number that identified that individual. Immobilized deer were kept under observation until capable of walking away from the capture area. Between June 1972-June 1976, 100 deer were captured and marked; 20-25 deer wore collars at any one time during the study.

Estimation of Population Size

The size of the CWTB herd was estimated using the cohort of collared deer in a tag-recapture method (Schnabel) in which we sampled animals by observation rather than by trapping. Marking was continuous during most of those months for which estimates were derived. A 14.8 km perimeter route and a 4.7 km route through the center of the Refuge allowed nearly complete visual sampling of the study area. Census data were collected by 2 observers who simultaneously drove their respective routes starting approximately 90 minutes before sunset. Three evening censuses were conducted during a 3-5 day period each census month, except in November 1974, January 1975 and November 1976, when only 2 censuses were run.

There are several statements or assumptions associated with a tag-recapture method for population estimation. These can be stated in the following way (Overton 1971:434):

1. There exists a well defined collection (population) of animals containing N individuals.
2. M of these individuals are marked, say with a tag.
3. There exists a sample of n "observations" of animals from the population, containing x observations of marked animals.
4. The average probability \bar{p}_m of observing a marked

animal is equal to the average probability \bar{p}_u of observing an unmarked animal. That is, $\bar{p}_m = \bar{p}_u$.

During a census period, each observer recorded the total number of marked and unmarked deer observed along his route, being careful not to tally the same deer more than once. After January 1975, both observers also recorded the identifying number of each collared deer, so that a history of "recapture" of all marked deer could be determined. Generally, censuses were conducted only during November-March, as sex and age classes were more equally visible, sample sizes were larger, and collared deer were less conspicuous relative to unmarked deer than during summer. Dense vegetation during May-October made those deer wearing white collars easier to locate visually than unmarked deer, a violation of Statement 4 above.

We attempted to classify each deer as to sex and age, but the large percentage of deer in the unknown category and the small number of collared deer in some of these cohorts precluded the use of these data in a stratified estimate of population size as employed by Strandgaard (1972). A population estimate was calculated for each of the 12 census periods (months) using a Schnabel estimate. The method and notation follow Chapman and Overton (1966:173). To estimate population size, we let

$$x = \sum_{i=1}^k x_i = \text{number of recaptures} \quad \text{Equation 1}$$

$$\lambda = \sum_{i=1}^k (n_i M_i) \quad \text{Equation 2}$$

where

x_i is the number of marked animals "captured" in the i^{th} day,

n_i is the total number "captured" in the i^{th} day,

M_i is the number of marked animals in the population on the i^{th} day.

Then

$$\hat{N} = \frac{\lambda}{x+1}. \quad \text{Equation 3}$$

Confidence limits for these estimates were constructed following Chapman and Overton (1966:174, Table 1) for $x \leq 50$, where x had approximately a Poisson distribution. When x was greater than 50, the maximum value tabled, it was necessary to use the normal approximation to the Poisson to obtain the lower (\underline{x}) and upper (\bar{x}) limit,

$$\underline{x} = (x+2) - 2\sqrt{x+1} \quad \text{Equation 4}$$

$$\bar{x} = (x+2) + 2\sqrt{x+1} \quad \text{Equation 5}$$

and solve the inequality for N :

$$P[\underline{x} \leq \frac{\lambda}{N} \leq \bar{x}] = 1 - \alpha. \quad \text{Equation 6}$$

To test for a statistically significant difference in population levels between years, we compared a Schnabel estimate (N_0) from 1975 with a comparable estimate (N_1) from 1976 and used the test statistic from Chapman and Overton (1966:175),

$$Z = \frac{x_0 - (x_0 + x_1) \frac{\lambda_0}{\lambda_0 + \lambda_1} \pm \frac{1}{2}}{\sqrt{(x_0 + x_1) \left(\frac{\lambda_0}{\lambda_0 + \lambda_1} \right) \left(\frac{\lambda_1}{\lambda_0 + \lambda_1} \right)}}. \quad \text{Equation 7}$$

Sex and Age Composition

Sex and age composition of the herd were derived from deer observed on census routes conducted during October-December. Each deer observed was classified as adult male, adult female, yearling male, yearling female, fawn or unknown and the size of each deer group was noted. A deer was considered to be a fawn from birth until 12 months old, a yearling from 12-24 months old and an adult if more than 24 months of age. An anniversary date of 1 June was used, even though we

knew some births occurred later in the summer. Criteria for classification included the presence or absence of antlers, relative size, general conformation of the body, the shape and length of the head, and behavior. Herd composition was determined during autumn, when sex and age classes were most identifiable. In late December-early January, males began dropping their antlers. Prior to October, both adult males and fawns were secretive and, therefore, not represented in herd composition counts in proportion to their abundance.

Collection of Mortality Data

From September 1974-March 1976, systematic searches of the entire study area were conducted to locate the remains of dead deer. These searches were usually done by 2 people who slowly walked through a predetermined search area until it was thoroughly covered. Approximately 20% of the 790 ha study area was searched each week with 15-30 man-hours spent in this activity weekly. We also located carcasses while engaged in other types of data collection, by observing the behavior of turkey vultures (Cathartes aura), and by reports from Refuge personnel. Additional carcasses were obtained from road kills, from deer illegally shot and left on the Refuge, and from deer killed during capturing and handling.

Once located, we described the physical condition of the carcass, sex and age of the animal, and mapped the location of the carcass on 21.5 cm X 28.0 cm aerial photographs of the study area. We also estimated the time of death as closely as possible based on decomposition of the carcass and the past search schedule for that area. In addition, we collected the skull, jaws and a femur marrow sample and, depending on the condition of the carcass, a sample of rumen contents and the female reproductive tract. If the deer had not been dead more than several days and was not scavenged, the entire carcass was taken for necropsy. Detailed necropsies were performed by veterinary pathologists under laboratory conditions on several occasions, but usually we examined carcasses in the field to determine the cause of death.

Bone marrow samples were frozen and later analyzed for fat content by the reagent-dry assay method (Verme and Holland 1973). To age the carcasses, we removed a tooth from the jaw or skull of each adult specimen and made a permanent slide of stained tooth sections using a slight modification of a method used by Lindzey and Meslow (1972:303-304). Slides were then examined with a binocular microscope at 20-60X and the cementum annuli were counted. Generally the p_2 was selected for aging, although other premolars and molars were used when the preferred tooth was missing. Yearlings and fawns could be aged by the wear and replacement method (Severinghaus 1949).

Indices of Home Range Size

During every month that one of us was on the Refuge, the location of each collared deer observed was plotted. The date, time and general activity (e.g., bedded, feeding) of the deer were noted as well as the sex and age of any deer associated with the marked individual. All locations were later assigned x-y coordinates from the grid system and used in calculations of home range size. We excluded those observations that occurred within 60 minutes of the previous location. This exclusion of data points (less than 10% of all observations) was necessary to minimize dependence between observations and to increase comparability among data sets for different deer. Generally, deer that lost their collars were eliminated from further observation and home range analysis, unless they could still be identified readily in the field by ear tags and/or ear streamers. Unless otherwise noted, only location data from deer that were observed in 4 or more months for a total of at least 20 locations were included in this analysis. Although an arbitrary decision, it was necessary to maintain comparability among individuals, our prime consideration in this section.

Indices of home range size were calculated by 2 independent methods. The first method consisted of connecting all the outermost points on a scattergram to form the smallest convex polygon that contained all capture points; the area of this polygon served as an index

of home range size (Jennrich and Turner 1969:228). After ordering the points of the polygon in a counterclockwise fashion about their geometric center, the area was computed using the formula

$$A = \frac{1}{2} \sum_{i=1}^n (x_i y_{i+1} - x_{i+1} y_i), \quad \text{Equation 8}$$

where (x_i, y_i) is the i^{th} ordered capture point from a total of n points and $(x_{n+1}, y_{n+1}) = (x_1, y_1)$.

The second method will be referred to as the determinant method. It was described by Jennrich and Turner (1969) who compared 4 methods of calculating size of home range, including both methods used here. This index was designed to measure non-circular as well as circular home ranges; it is not subject to sample size bias as the convex polygon approach. This index is computed by the formula

$$A = 6\pi |S|^{1/2}. \quad \text{Equation 9}$$

Here, S is the determinant of the covariance matrix of the capture (= observation) coordinates

$$S = \begin{pmatrix} s_{xx}^2 & s_{xy} \\ s_{yx} & s_{yy}^2 \end{pmatrix} \quad \text{Equation 10}$$

where s_{xx}^2 = variance of x , s_{yy}^2 = variance of y and $s_{xy} = s_{yx}$ = covariance of x and y .

Jennrich and Turner (1969:232) first assumed that a bivariate normal distribution described the intensity with which an animal utilizes each point in its habitat. They then defined the home range of an individual as "the area of the smallest sub-region which accounts for a specified proportion, p , of its total utilization." The value of p is arbitrary, but when equal to 0.950, the constant in Equation 9 is equal to 6. Thus, Equation 9 becomes the area of the smallest region that accounts for 95% of an animal's utilization of its habitat. Actually, both Equations 8 and 9 need to be multiplied by 0.087 to give the area

of the home range in hectares, as derived from the scale of our grid system.

RESULTS AND DISCUSSION

Columbian White-tailed Deer-
Habitat Relationships

Forage quality and availability. Since food habits of CWTD had not been studied, we did not know exactly which plant species were selected by whitetails when feeding. Suring (1974) reported that 99% of all feeding deer observed during 1972-73 were grazing on herbaceous vegetation (N = 14085), instead of browsing on woody plants. An examination of 4 CWTD stomachs by Scheffer (1940:277) in December 1939-January 1940 revealed that "all were at least half-full of soft grass and contained no traces of woody plants." Rumen contents collected from 1972-77 during all seasons from 33 whitetails were composed almost exclusively of herbaceous vegetation (Gavin, unpublished data).

Recent studies indicated the potential importance of grasses and forbs to white-tailed deer in North America. They totalled 60% of the diet by volume of Indiana deer during January-March (Sotala and Kirkpatrick 1973), 41% of the total forage ingested by Arkansas deer in March (Segelquist et al. 1972), and grasses and forbs comprised as much as 50% and 40%, respectively, of the winter diet of Michigan's George Reserve deer during periods of no snow cover (Coblentz 1970). Whitetails grazed extensively in grassy fields for 8-10 months of the year in Ohio (Harder and Peterle 1974) and were found to utilize herbaceous forage in significant amounts at least seasonally in Wisconsin (McCaffery et al. 1974), Montana (Allen 1968) and Arizona (Anthony and Smith 1977). On our study area, whitetails grazed throughout the year despite the availability of trees and shrubs (i.e., Symphoricarpos, Sambucus, Cornus, Salix and Rubus) that are browsed by white-tailed deer elsewhere (Allen 1968, Hosley 1956:205, Skinner and Telfer 1974: 211).

Water foxtail (Alopecurus geniculatus), one of the few native species of grass on the Refuge, was distributed over the entire study area in monospecific patches several meters in diameter; we often observed CWTD grazing this grass. Although its importance in their

diet was not clear, water foxtail remained green and lush throughout the year. This species was heavily utilized by cattle, but was little affected by haying since it only attained a height of 15-20 cm. Hitchcock and Cronquist (1973:620) stated that species of Alopecurus "are highly palatable and nutritious, but rarely abundant enough to constitute an appreciable element of the range forage." Although large patches of water foxtail would be periodically covered by standing water during winter, the Refuge was an exception to the generalization regarding abundance of this plant.

Limited qualitative analysis of water foxtail provided some insight into its characteristics. Percentage dry matter was determined by the ratio of the weight of a sample of grass after drying in an oven at 80-90 C to the weight of that same sample before drying. Crude protein content and dry matter digestibility were estimated using a micro-Kjeldahl technique (AOAC 1970) and the method of Tilley and Terry (1963), respectively. Samples were analyzed from 4 fields, 2 of which were cut for hay and 2 were grazed by cattle. The seasonal pattern and approximate percentages were the same for each field regardless of treatment and results were therefore combined (Table 2). Mean values ranged from 18.8 (June)-27.0 (January) for crude protein, 65.9 (June) - 70.6 (November) for dry matter digestibility and 21.7 (January) - 26.8 (August) for dry matter content. In general, crude protein increased, dry matter decreased and digestibility remained constant from summer to winter.

French et al. (1955) found that 6-7% protein in the diet of male white-tailed deer was sufficient for maintenance needs and 13-16% provided optimal body growth and antler development. Ullrey et al. (1967: 682) concluded, however, that male fawns have a higher dietary protein requirement than female fawns for maximum weight gain during the immediate post-weaning period. A crude protein concentration of 12.7% was adequate for females, but not for males. A concentration of 20.2%, the next highest crude protein concentration used in their feeding trials, appeared adequate for male fawns. In another study, productivity, survival and condition of breeding females were adversely

Table 2. Dry matter content, crude protein content and dry matter digestibility of water foxtail (*Alopecurus geniculatus*) collected from the CWT National Wildlife Refuge, June 1975-March 1976.

	Dry matter (%)			Crude protein (%)			Digestibility (%)		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
June	25.3	1.7	12	18.8	1.1	4	65.9	2.3	4
August	26.8	2.8	12	20.5	1.8	3	67.0	0.8	3
September	23.5	1.0	12	23.1	2.8	4	66.4	0.7	4
November	24.7	2.1	12	26.9	2.2	4	70.6	2.9	4
January	21.7	2.3	12	27.0	2.3	4	67.5	2.5	4
March	22.0	2.6	12	24.0	1.8	4	69.5	1.6	4

affected by a diet containing 7% or 11% protein when compared to a diet with 13% (Murphy and Coates 1966). Nitrogen (crude protein) content is, of course, only 1 attribute used to determine forage value of a feed. However, Cowan et al. (1970:50) believed that since there is a high positive correlation between nitrogen content and digestibility of energy, "it may be safe to predict that if the combination of natural foods eaten by a deer contains an adequate percentage of crude protein, other nutritional requirements probably will be incidentally covered."

It appeared, then, that the qualitative characteristics of water foxtail that we examined were excellent, and that CWTD preferred to graze rather than to browse. Although we were not sure which herbaceous species these deer actively selected, if any, it is reasonable to assume that if water foxtail was not selected, then forage even more palatable or nutritious was probably eaten, an assumption for which some evidence does exist (Longhurst et al. 1968:186, Swift 1948, Nagy et al. 1969). Unless there was a micro-nutrient deficiency in the Refuge vegetation, a possibility in an area with such high rainfall, there was no apparent reason why CWTD should suffer from nutritional stress.

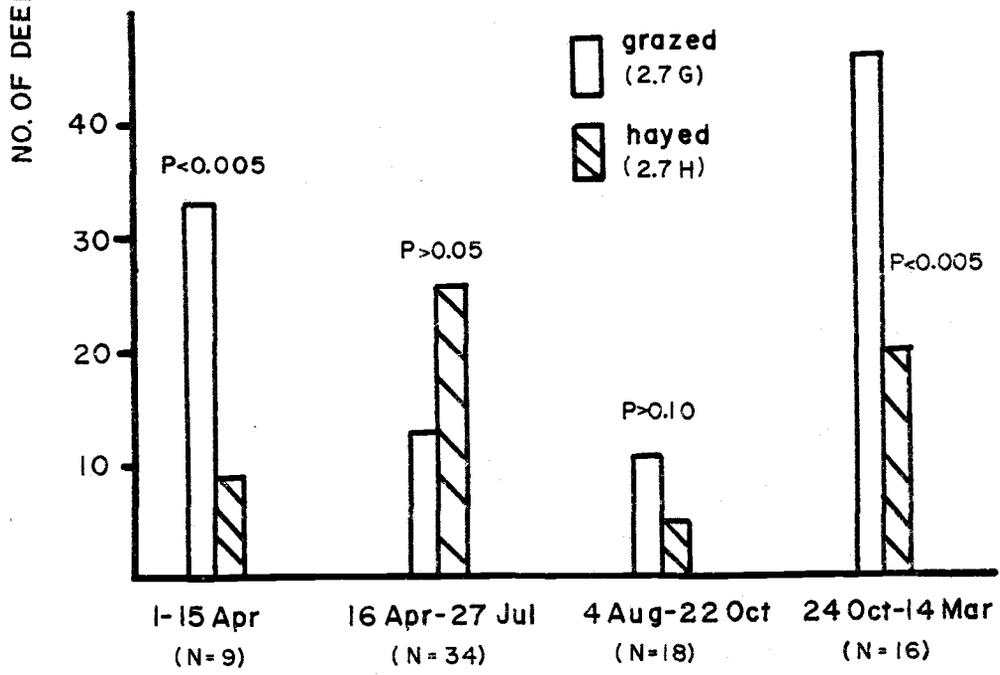
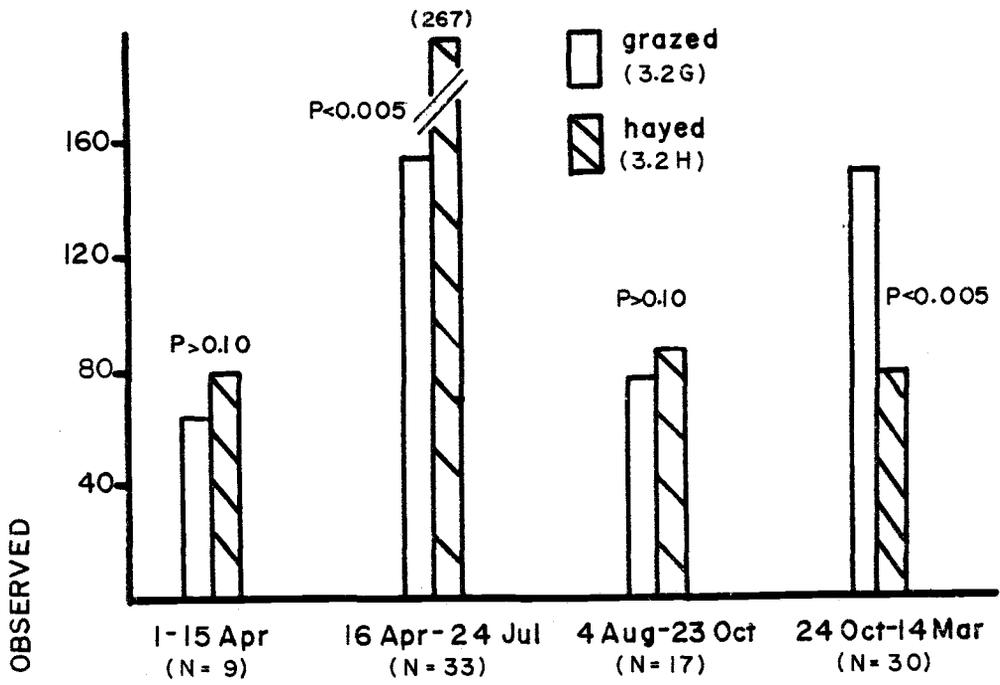
Habitat use. Data collected in 1972-73 indicated that plant communities on the Refuge that provided cover taller than 70 cm in the vicinity of forage were more heavily utilized than communities that provided cover or forage alone (Suring and Vohs, in press). Open canopy forest or dense thistle (Cirsium arvense) communities were preferred to closed canopy forest or improved pasture, for example. Whitetails avoided close association with cattle even though large numbers of cattle were present on the study area most of that year; only 7% of the observations of feeding deer were within 30 m of cattle (Suring 1974).

From April 1975-March 1976 we tallied the number of whitetails observed on each of the 4 fields from which water foxtail samples were collected, to evaluate the effects of haying and livestock grazing on deer use. Unit 2.7 (9.1 ha) had been cut for hay in 1974, but was bisected by a fence for this 1975 experiment, with deer use on the half that was grazed by cattle (2.7G) compared to the half that was cut for

hay (2.7H). The same approach was taken with unit 3.2 (14.8 ha), except this field had been grazed in 1974. White-tailed deer had easy access to all of these fields, since fencing consisted of 3-strand barbed wire only 1.5 m high. The bottom strand was high enough above the ground that deer usually entered these fields by going under this strand. Cattle were placed on 2.7G and 3.2G on 15 April and removed in late October, with a stocking rate of about 2.5 head per hectare in each pasture. Unit 2.7H was cut for hay twice, 27 July and 23 September. Unit 3.2H was cut for hay only once beginning on 24 July. All deer in each field of a pair were counted during a predetermined sampling period; usually we sampled both pairs of fields simultaneously since they were adjacent to each other. Most sampling occurred in the evening when deer were actively grazing, but samples were taken throughout the 24-hour daily period.

Total deer tallied in 77 samples for unit 2.7 and 89 samples for unit 3.2 were 163 and 968, respectively. After grouping the samples into meaningful periods, based on the presence or absence of cattle and the timing of haying, we compared use within each pair of fields using a G-test for goodness of fit (Fig. 4). Two patterns were consistent in each pair of plots: 1) Whitetails avoided pastures containing cattle (2.7G and 3.2G) for 2-3 months after cattle were moved onto them. The preference for the non-grazed field during this time was highly significant in the comparison of 3.2H and 3.2G ($G = 29.462$, $df = 1$, $P < 0.005$); no preference had been shown for either field prior to the presence of cattle ($G = 1.541$, $df = 1$, $P > 0.10$). Although preference for 2.7H was not statistically significant from mid-April to late July when cattle were present on 2.7G ($G = 3.752$, $df = 1$, $P > 0.05$), deer had shown a strong preference for 2.7G prior to the presence of cattle ($G = 13.315$, $df = 1$, $P < 0.005$). 2) After removal of cattle from the Refuge in October, whitetails selected those fields that had been grazed by cattle in preference to hayed fields. The preference was highly significant for both 3.2G over 3.2H ($G = 22.175$, $df = 1$, $P < 0.005$) and for 2.7G over 2.7H ($G = 9.709$, $df = 1$, $P < 0.005$) and continued until the end of the experiment in mid-March 1976. This second result suggested that

Figure 4. Comparison of white-tailed deer use of pastures that were hayed or grazed by cattle on the CWT National Wildlife Refuge mainland in 1975. (Unit 3.2 had a history of being grazed by cattle; unit 2.7 had a history of being cut for hay. N is the number of observation periods).



the extremely disproportionate use of unit 3.2 over unit 2.7 during 1975-76, as evidenced by the mean number of deer observed per sample (i.e., 10.9 and 2.1, respectively), may have been an active preference for a field with a history of livestock grazing prior to the experiment. Unit 2.7 had a history of being cut for hay prior to 1975.

The relationship between deer use and cattle on the Refuge seemed paradoxical. Deer tended to avoid cattle and their pastures during summer, but preferred to graze in those same fields when cattle were absent during fall and winter. Quantitative measurements were not taken, but pastures that were grazed by cattle appeared to maintain higher plant diversity than did fields that were cut for hay. Some species, such as white clover (Trifolium sp.), disappeared relatively soon after cattle grazing was eliminated. Cattle grazing was also a more efficient method of keeping pasture vegetation short and actively growing; reducing plant biomass was a much greater management problem on the Refuge than having too little. Vegetation that was mechanically cut once or twice during summer had time enough to grow between the last cutting and dormancy in the fall. Thus, grass in fields that were mechanically cut was much taller (and presumably less palatable) during winter than vegetation that had been grazed by cattle until late October.

Recent findings that Thomson's gazelles (Gazella thomsonii) in Tanzania preferred to graze in areas with vigorous regrowth and high forage density that resulted from the grazing of migratory wildebeest (Connochaetes taurinus) (McNaughton 1976) seem analogous to the relationship of CWTB and cattle on the Refuge. Bell (1970) obtained similar results with a multi-species system of grazing ungulates on the Serengeti. Domestic cattle were intentionally used to graze herbaceous vegetation in northeastern Oregon from 1963-74 to improve the quality of winter forage for elk, which resulted in more than a 10-fold increase in elk-days of use (Anderson and Scherzinger 1975).

Summary. Abundant observations of CWTB and preliminary examination of their rumen contents indicated that these deer fed almost exclusively

on herbaceous vegetation. This vegetation was apparently of high quality, easily available to deer on the Refuge and preferred over several species of shrubs and trees often utilized by white-tailed deer elsewhere. Haying or grazing by domestic cattle was needed to maintain high forage quality in open pastures. Although CWTD avoided close physical proximity to cattle, whitetails preferred to feed in pastures that had been grazed by cattle.

Population Size

Historical stability. Scheffer (1940) estimated the number of white-tails in the area now encompassed by the Refuge mainland at 250-350 in 1939, based on a reconnaissance of the area and interviews with local farmers. During the same year, Lauckhart (1940) obtained from a "local game protector" an independent estimate of 400 whitetails in Wahkiakum County, half of which were on Puget Island and half within Diking District #4. The diking district included the present study area, while the Puget Island population was considered separate and distinct from the Refuge herd (Gavin 1978). To our knowledge, no estimates were actually based on extended field work until Suring (1974) estimated the study area population at 200-230 in the winter of 1972-73. His estimate was derived from evening and spotlight counts and daily observation of the herd. From 1974-77, our estimates in November ranged from a high of 214 in 1974 to a low of 164 in 1976, using a Schnabel method (Table 3).

Although the estimates obtained prior to 1974 were not derived using any rigorous estimation technique, they have value in establishing the magnitude of past fluctuation in this population. We can not be sure that this population did not fluctuate violently between 1940 and 1972, but our discussions with former landowners never disclosed any indication of large scale fluctuations as evidenced by whitetail scarcity or mortality (i.e., die-offs). Our estimates suggested that annual fluctuations about the mean of the wintering population (1972-77) were on the order of 10-15%.

Table 3. Population estimates of white-tailed deer on the CWT National Wildlife Refuge (Washington mainland).

<u>Year</u>	<u>Estimate</u> ^a	<u>Technique</u>	<u>Source</u>
1939	250-350	Interviews	Scheffer (1940)
1939	200	"	Lauckhart (1940)
1972-73	200-230	Spotlight-evening counts	Suring (1974)
1974 (Nov)	214 (127-370)	Schnabel	This study
1975 (Nov)	180 (124-265)	"	"
1976 (Nov)	164 (92-306)	"	"
1977 (Nov)	202 (126-333)	"	"

^aConfidence intervals (95%) are in parentheses.

Schnabel estimates. We obtained 11 monthly estimates of population size between November 1974-November 1976 and an additional estimate in November 1977. The estimates (Table 4) were calculated using 3 slightly different sets of data according to the length of time over which those data were accumulated: daily estimates that used only data collected on that day, monthly estimates that used all the data collected only during that month, and a "running" Schnabel estimate that was calculated after the addition of each month's data to the previous month's data. This last estimate was accumulated for each of 2 periods, November 1974-May 1975 and November 1975-March 1976, and had the effect of smoothing the monthly estimates.

It was apparent while we were in the field and it appeared from a graph of the "running" Schnabel estimates that the population experienced a general decline from November 1974 to March 1976 (Fig. 5). To test for a difference in population levels statistically, we used census data from February-March 1975 to calculate a Schnabel estimate that we compared to an estimate based on the data from February-March 1976. The data, taken from Table 4, resulted in $\hat{N} = 215$, $\lambda = 21016$ and $x = 97$ for 1975 and $\hat{N} = 160$, $\lambda = 16440$ and $x = 102$ for 1976. The resultant Z value (2.03) corresponded to a probability level of 0.0212 (Steel and Torrie 1960:434): the population was significantly larger in February 1975 than in February 1976. The mean number of deer observed per census (January-March) decreased from 131 (SD = 28.6) in 1975 to 115 (SD = 14.3) in 1976.

The choice as to which data to use to test for a difference in population levels between years was an ad hoc decision; it was made after population estimates had been calculated. However, we were most concerned with choosing comparable time periods to make the test and, therefore, chose the February-March interval for the following reasons:

1. Our data indicated that most winter mortality occurred prior to this period, so that population estimates at this time approximated the number of successful overwintering deer.
2. This bimonthly period contained the same number of census days (6) each year.

Table 4. Schnabel estimates of white-tailed deer on the CWTB National Wildlife Refuge (Washington mainland) and pertinent data used to derive those estimates.^a

	M_i	n_i	x_i	\hat{N}	"running" Schnabel
<u>1974</u>					
Nov 5	20	87	5	290	<u>1974-75</u>
Nov 17	21	90	11	158	
	$\hat{N} = \lambda = 3630$ (127-370)				$\hat{N} = \lambda = 3630$ (127-370)
<u>1975</u>					
Jan 2	21	108	12	174	$\hat{N} = \lambda = 8229$ (152-296)
Jan 3	21	111	10	212	
	$\hat{N} = \lambda = 4599$ (129-317)				
Feb 15	25	173	14	288	$\hat{N} = \lambda = 20129$ (193-298)
Feb 16	25	158	17	219	
Feb 17	25	145	15	227	
	$\hat{N} = \lambda = 11900$ (188-344)				
Mar 19	26	86	11	186	$\hat{N} = \lambda = 29255$ (182-257)
Mar 20	26	138	20	171	
Mar 21	26	127	20	157	
	$\hat{N} = \lambda = 9126$ (135-237)				
May 5	22	133	11	244	<u>$\hat{N} = \lambda = 37769$ (184-248)</u>
May 6	22	128	17	156	
May 7	22	126	14	185	
	$\hat{N} = \lambda = 8514$ (145-273)				

Table 4. continued.

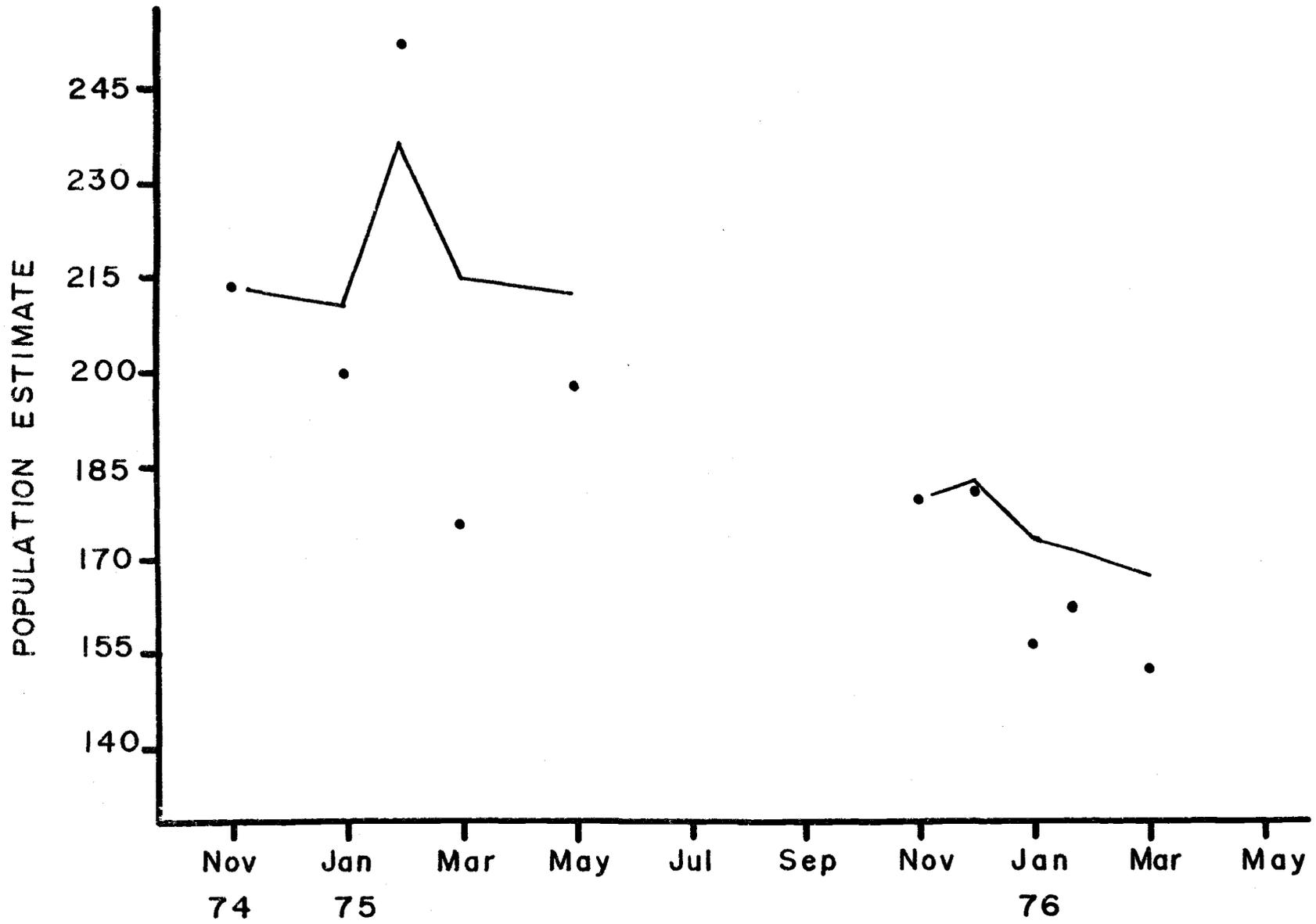
	M_i	n_i	x_i	\hat{N}	"running" Schnabel
<u>1975</u>					
Nov 18	22	97	11	178	
Nov 19	22	72	8	176	
Nov 20	22	85	11	156	
				$\lambda = 5588$	
				$\hat{N} = 180$ (124-265)	$\hat{N} = 180$ (124-265)
					<u>1975-76</u>
Dec 16	22	94	12	159	
Dec 17	22	123	15	169	
Dec 18	22	137	15	188	
				$\lambda = 7788$	
				$\hat{N} = 181$ (132-250)	$\hat{N} = 183$ (147-235)
<u>1976</u>					
Jan 26	23	114	16	154	
Jan 27	23	122	18	148	
Jan 28	23	113	16	153	
				$\lambda = 8027$	
				$\hat{N} = 157$ (118-211)	$\hat{N} = 174$ (146-210)
Feb 16	24	131	18	165	
Feb 17	24	93	18	117	
Feb 18	24	135	16	191	
				$\lambda = 8616$	
				$\hat{N} = 163$ (126-218)	$\hat{N} = 172$ (148-201)
Mar 10	24	96	16	136	
Mar 11	24	109	17	145	
Mar 14	24	121	17	161	
				$\lambda = 7824$	
				$\hat{N} = 153$ (115-205)	$\hat{N} = 168$ (148-193)

Table 4. continued.

	M_i	n_i	x_i	\hat{N}
<u>1976</u>				
Nov 20	20	65	8	144
Nov 21	20	50	5	167
		$\lambda = 2300$		
		$\hat{N} = 164$		(92-306)
<u>1977</u>				
Nov 25	17	81	7	172
Nov 26	17	79	4	269
Nov 27	17	78	8	147
		$\lambda = 4046$		
		$\hat{N} = 202$		(126-333)

^a M_i is the number of collared deer in the population, n_i is the total number of deer observed during census, and x_i is the number of collared deer observed during census. $\hat{N} = \lambda/x+1$, where $\lambda = \sum_{i=1}^k (n_i M_i)$ and $x = \sum_{i=1}^k x_i$. Confidence intervals (95%) in parentheses.

Figure 5. Monthly estimates of population size of white-tailed deer on the CWT National Wildlife Refuge mainland, with "running" Schnabel estimates (solid lines) for 2 periods, November 1974-May 1975 and November 1975-March 1976.



3. The sampling period was short enough (30-35 days) to minimize population changes that would violate Statement 4 of the tag-recapture method.

4. In both years, both census takers recorded collar numbers from marked deer that were sampled during this bimonthly period. This information was used to evaluate observability of marked deer by sex and age.

Examination of tag-recapture method. Accurate population estimates from tag-recapture techniques are notoriously difficult to achieve. Tag-recapture methods probably result in conservative estimates of true population size when "recaptures" consist of observations of conspicuously marked individuals. In fact, 1 spotlight count of the entire study area in January 1976 resulted in a higher number of deer actually seen (174) than the estimate for that month (157). Although this was the only month this happened, it indicated to us that the estimates were generally conservative and that we violated an assumption of the estimation method.

It is virtually impossible to directly examine the necessary equality of Statement 4, $\bar{p}_m = \bar{p}_u$, since we could not determine the average probability of observing an unmarked deer (i.e., \bar{p}_u). We could, however, examine equal observability among the marked cohort. Due to extensive daily observations of collared deer, and the efficient discovery of lost collars and carcasses of marked deer, we knew with certainty which collared deer were present in the population for every month that we computed an estimate (Appendix B). The following analyses were applied only to the February-March census data, since estimates used in the statistical comparison were derived from that period.

We grouped all collared deer by sex and tested for a statistical difference in observability between sexes by using a G-test with Yates' correction for small sample size. The same deer were then grouped by age and a similar G-test conducted. Neither the observability by sex ($P > 0.10$) nor age ($P > 0.10$) was significantly different in 1975 (Table 5). In 1976, observability of males compared to females was far from a

Table 5. Comparison of observability of collared white-tailed deer by sex and by age during February-March on the CWTD National Wildlife Refuge (Washington mainland). (Proportion of total in parentheses).

	<u>No. observed^a</u>	<u>1975 No. not observed^b</u>	<u>Totals</u>
Males	37.5 (0.63)	22.5 (0.37)	60
Females	$\frac{51.5}{89.0}$ (0.55)	$\frac{41.5}{64.0}$ (0.45)	$\frac{93}{153=N}$
G=0.764, df=1, P>0.10 ^c			
Adults	44 (0.52)	40 (0.48)	84
Yearlings	16 (0.59)	11 (0.41)	27
Fawns	$\frac{29}{89}$ (0.69)	$\frac{13}{64}$ (0.31)	$\frac{42}{153=N}$
G=3.270, df=2, P>0.10			
	<u>No. observed^a</u>	<u>1976 No. not observed^b</u>	<u>Totals</u>
Males	25.5 (0.71)	10.5 (0.29)	36
Females	$\frac{73.5}{99.0}$ (0.68)	$\frac{34.5}{45.0}$ (0.32)	$\frac{108}{144=N}$
G=0.098, df=1, P>0.50 ^c			
Adults	61.5 (0.64)	34.5 (0.36)	96
Yearlings	$\frac{37.5}{99.0}$ (0.78)	$\frac{10.5}{45.0}$ (0.22)	$\frac{48}{144=N}$
G=3.055, df=1, P>0.05 ^c			

^aTotal number of collared deer observed during 6 censuses.

^bNumber of times collared deer were present in population during 6 censuses, but not observed.

^cYates' continuity correction applied to this test.

significant difference ($P > 0.50$), but when these same deer were grouped into age classes, they exhibited a difference in observability much greater than that between sexes, though still not significant ($P > 0.05$). Because there were no collared fawns present in 1976, this test compared only adults and yearlings.

Variation in observability among sex and age classes of deer has generally been considered a significant bias, at least seasonally, in population analysis (Downing et al. 1977, Strandgaard 1972). However, we concluded that if observability by sex and age did not differ significantly during February-March, then the advantages in using a stratified index as suggested by Overton (1971:437) would be minimized. That is, it was not necessary to have some minimum number of deer marked in each sex and age class, nor was it necessary to classify each deer observed during sampling by sex and age.

There may have been, however, significant differences in observability among individuals that were not detected by examining sex and age classes of marked deer. This would have been important to estimation of population size only if it resulted in an inequality in the mean probability of observing marked as compared to unmarked deer. The possibility of such biases did exist. However, population estimates calculated for the bimonthly period each winter and used to test for a population decline over that year were based on a marked sample of 27 deer in 1975 and 24 deer in 1976. Fourteen of these deer were marked throughout both winters, which should have increased the comparability of those 2 data sets (Appendix B).

The mean probability of observing any marked deer during each of the bimonthly periods could be determined, since M_i and x_i were known for each census day (in Table 4). The mean probability of observing a collared deer increased from 0.634 in 1975 to 0.708 in 1976. Although not a significant difference ($G = 1.860$, $df = 1$, $P > 0.10$), we were not able to account for the increase. This increase in mean observability of marked deer would have resulted in lower population estimates in 1976 relative to 1975 (i.e., on the order of 20 deer less), unless there had been a corresponding increase in observability of unmarked

deer. We felt this was unlikely, so that the decrease in population from February 1975 to February 1976 (i.e., 215 to 160), although a real trend, was probably not as great as indicated.

Summary. Available information indicated that the size of this population was relatively stable since at least 1939. From 1972-77, population size in winter fluctuated only 10-15% about the mean population size for those years. The number of deer seen per census route and the Schnabel estimates suggested that a decline in population size occurred from 1974-76. Examination of the data used in the estimation technique revealed that although the downward trend was statistically significant, it may not have been as pronounced as was indicated by the Schnabel estimates.

Population Characteristics

Density. White-tailed deer density on the 790 ha study area in late winter ranged from 30.0 deer/km² in 1975 to 21.3 deer/km² in 1976, using the "running" Schnabel estimates. This was a mean density over the entire study area and included large tracts where deer were not found except during the evening feeding time. A more meaningful density figure of 42.0 deer/km² was obtained for the Refuge in November 1975, after deleting fields that provided no cover and contained no deer during the daylight hours (e.g., fields that had been cut for hay). That is, during November 1975, 180 deer (from estimates) spent most of the diurnal period within 429 ha of the study area. Refuge unit R4 (44.3 ha), which was delineated by natural and man-made boundaries, was known to contain at least 41 deer in March 1975, an effective density of 93.2 deer/km². These latter estimates of density, when coupled with data on dispersion, provided a truer picture of the potential for density-dependent phenomena than the mean density estimate for the entire area.

We considered this population to be dense, but non-hunted populations of white-tailed deer in other areas have attained similar or higher densities. Approximately 39 deer/km² were found in Texas on

both the Aransas National Wildlife Refuge (White 1973) and Welder Wildlife Refuge (White et al. 1972). The highest density of whitetails, to our knowledge, occurred on the National Aeronautics and Space Administration's Plum Brook Station in northern Ohio. Total population size was estimated at 2499 deer, a density of 115 deer/km² (Rice and Harder 1977). The Key Deer, however, only attained a density of about 8-10 deer/km² on Big Pine Key (Hardin et al. 1976).

Dispersion. From June 1972-June 1973, approximately 18000 locations of whitetails were recorded on the Refuge during morning and evening feeding periods. The total number of deer observed, after weighting for sampling intensity, differed significantly ($P < 0.005$) among 3 Refuge areas that were chosen by dividing the study area into 3 nearly equal sections from west to east (Table 6). In addition, the number of deer per hectare was significantly correlated ($r = 0.999$) with the percentage of each section in woodland cover.

Computer printouts of Refuge schematics illustrated the number of CWTB by sex and age that were observed in each quadrat of the study area by season. Each quadrat was approximately 1.3 ha in area; we determined the 6 contiguous quadrats containing the greatest number of adult and yearling males observed, for example, as that area (approximately 1% of total study area) with the highest density of males. Figures 6-8 show the 3 most dense areas (i.e., about 3% of study area) for each class; since the 3 highest areas of concentration were the same for females and for all deer, Fig. 6 sufficed for both these classes. Each area of high density was adjacent to a woodlot, which reflected the tendency of these deer to feed close to cover.

Differences in sampling intensity over the Refuge during the year prevented among-season comparisons of dispersion within 1 sex or age class. We were limited, therefore, to within-season comparisons among sex and age classes, which would not be affected by that bias. Winter was excluded due to the difficulty of classifying each deer by sex. During June 1972-June 1973, the 3 highest density areas (i.e., each area containing 6 contiguous quadrats) contained 19.9% of all

Table 6. Dispersion of white-tailed deer on the CMTD National Wildlife Refuge mainland, June 1972-June 1973.

<u>Unit</u>	<u>Area (ha)</u>	<u>Woodland (%)</u>	<u>No. of observations</u>	<u>Corrected no. of observations^a</u>	<u>Corrected no. per hectare^b</u>
West	251.6	22	8060	9223	36.7
Center	270.7	31	7774	15532	57.4
East	<u>267.8</u>	13	<u>1976</u>	<u>3266</u>	12.2
Total	790.1		17810	28021	

^aActual number of observations was corrected by the proportion of observation periods spent in that unit.

^bDispersion of deer differed significantly among units ($G=8700$, $df=2$, $P<0.005$). Correlation of the corrected number of observations per hectare with percent of each unit in woodland cover resulted in $r=0.999$ ($P<0.05$).

Figure 6. The 3 areas (each 1% of Refuge mainland) of highest density of yearling and adult white-tailed deer females, as well as all sex-age classes combined, based on total observations during June 1972-June 1973. (Refuge mainland partitioned into west, center and east sections for analysis in Table 6).

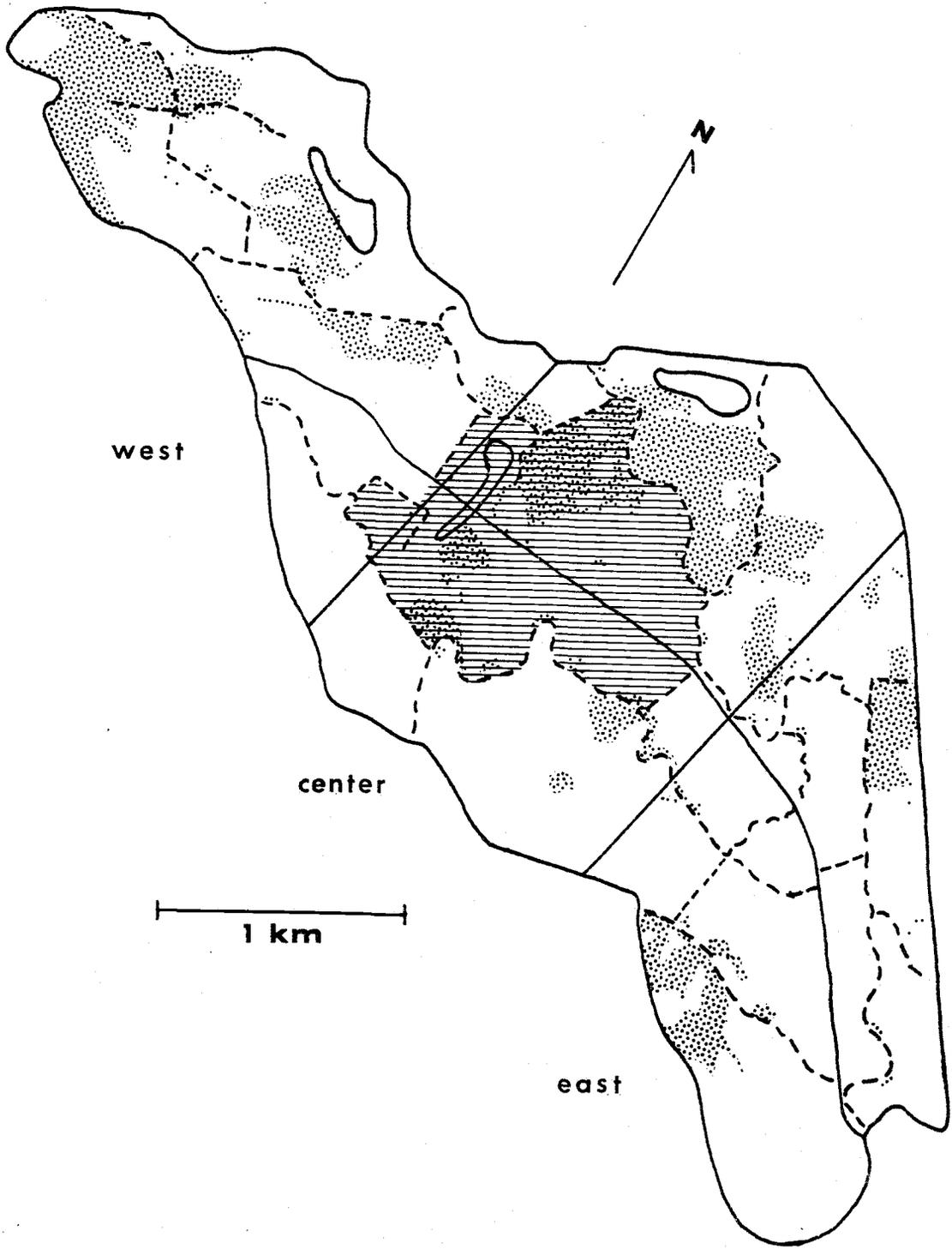


Figure 7. The 3 areas (each 1% of Refuge mainland) of highest density of yearling and adult white-tailed deer males, based on total observations during June 1972-June 1973. (During February 1975-March 1976, 63.0% of all buck groups observed were located in 2 larger areas).

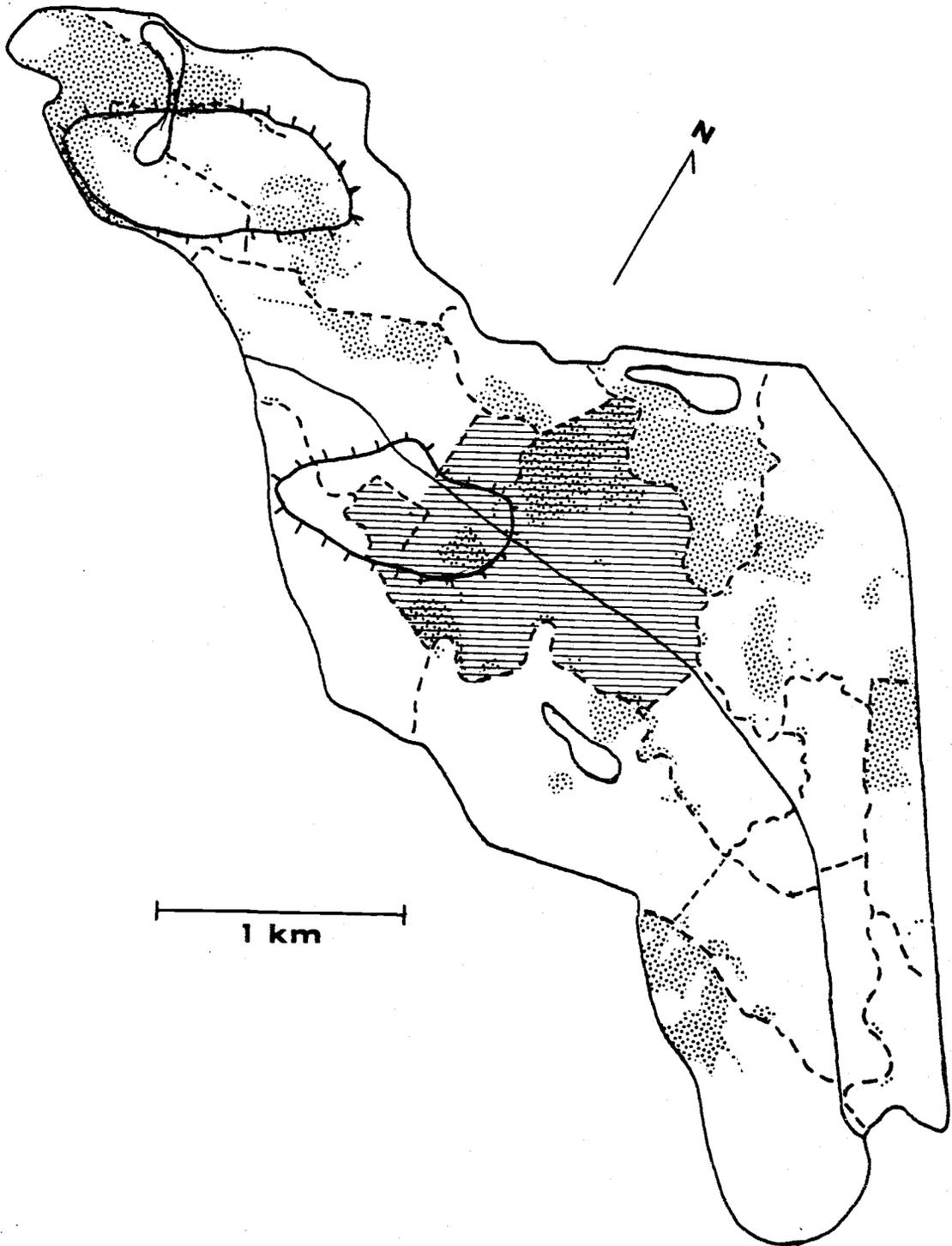
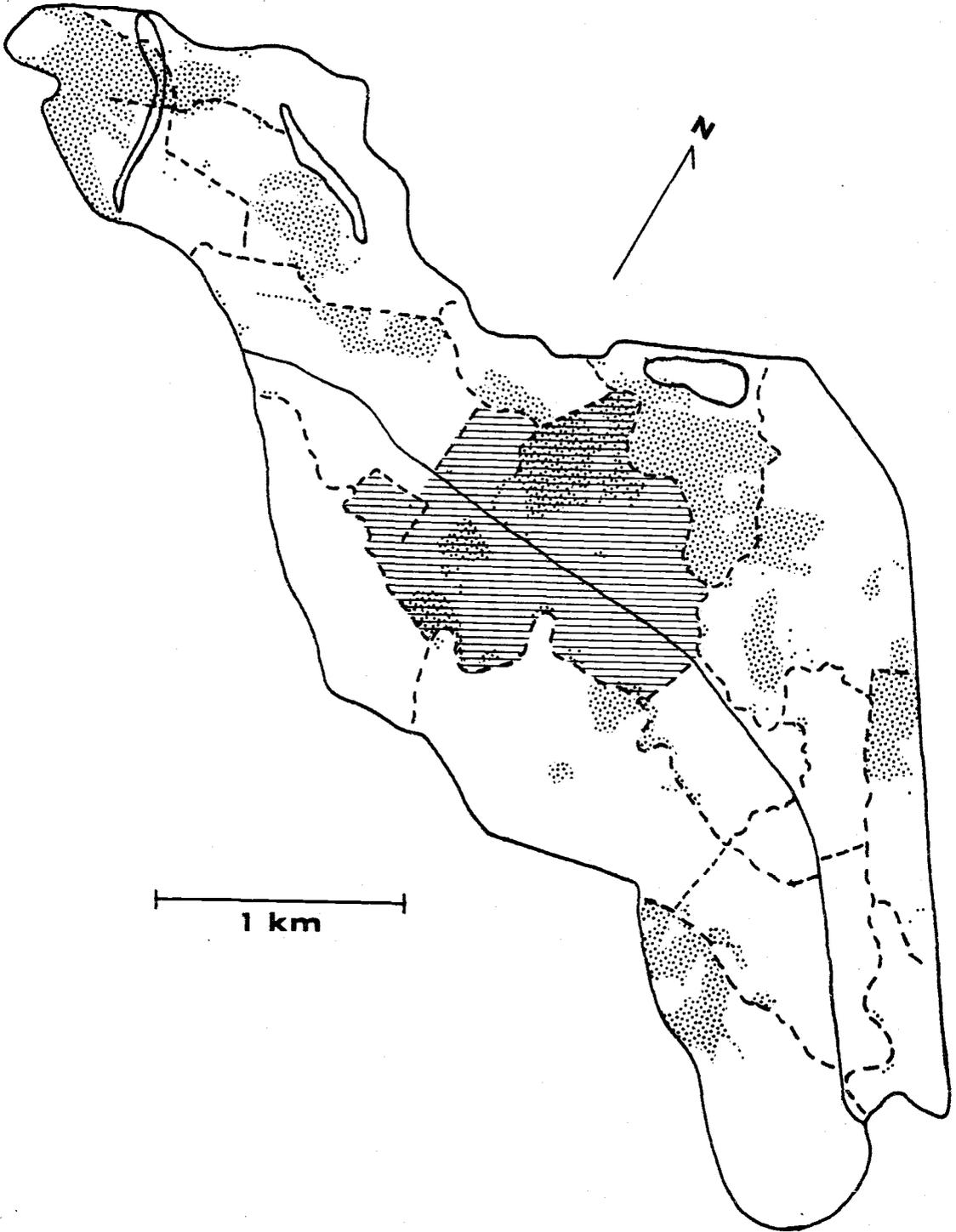


Figure 8. The 3 areas (each 1% of Refuge mainland) of highest density of white-tailed deer fawns, based on total observations during June 1972-June 1973.



deer observed, while the comparable percentages for females, males and fawns were 21.5, 25.9 and 23.5, respectively (Table 7). Bucks exhibited a more clumped dispersion than did does or fawns regardless of whether 3 or 6 areas with the highest densities were included. The percentage of each class observed for the entire year on these high density areas was always less than the percentage by season, since the areas of high concentration were not exactly the same among seasons for a given class.

The locations of these high density areas based on yearly totals were not exactly the same for each sex and age class, although there was complete agreement between them for females and for all deer. This was not surprising since females comprised about 59% of the entire population (see Table 10). Two of 3 areas of highest fawn concentration were identical with female areas and with buck areas, while bucks and does had only 1 high density area in common. It was interesting that all 3 areas for females and fawns were not "sympatric," which suggested that success in bearing and/or raising fawns was not equal over the entire study area.

Although comparable data were not collected after 1973, it was apparent that a clumped dispersion pattern continued throughout the study. Dispersion of buck groups observed from February 1975-March 1976 was highly contagious. A buck group was defined as an aggregation of deer that contained 3 or more males at least 1 year old. Although lone males were often difficult to classify by sex when they were antlerless, groups of such males were relatively easy to locate. Of 163 buck groups observed, 102 (63.0%) were seen in 2 areas that together encompassed about 15% of the study area (Fig. 7). This did not reflect, of course, the dispersion of all males on the Refuge, since those alone and in pairs were not included. It did indicate that either existing buck groups were attracted to these areas or that individual males formed such groups after moving into an area of high male density.

Sex ratios. We have few data on the primary or in utero sex ratio of CWTD. Two adult females that were illegally shot in February 1975 were pregnant with twins; each carried 1 male and 1 female fetus.

Table 7. Percentage of all observations of white-tailed deer that were observed on the 3 and 6 most dense "parcels" of the CWT National Wildlife Refuge mainland, June 1972-June 1973.^a

Season	Bucks			Does			Fawns		
	3%	6%	N	3%	6%	N	3%	6%	N
1972 Jul-Sept	37.9	54.6	1135	26.1	44.0	2488	33.4	54.7	437
Oct-Dec	37.1	51.4	940	23.1	41.3	3044	28.0	46.3	860
1973 Jan-Mar	--	--	-- ^b	--	--	-- ^b	31.6	49.8	570
Apr-Jun	36.4	53.7	841	27.3	43.3	2660	--	--	-- ^c
All year	25.9	39.5	3231	21.5	34.0	12359	23.5	39.7	2073

^aA parcel contains 1% of the study area. For example, 37.9% of 1135 bucks that were observed during summer were observed on 3% of the study area; 54.6% were observed on 6% of the study area.

^bWinter was excluded due to difficulty in classifying deer by sex.

^cSpring was excluded due to difficulty in classifying fawns from older deer.

Sex ratio of fawns during the neonatal period was determined by sexing those captured or found dead during summer. Sample sizes were too small in any 1 year for a meaningful statistical analysis, but we found no significant difference from a 1:1 sex ratio for the combined data for 1972-77 ($G = 0.280$, $df = 1$, $P > 0.50$). Nineteen of 39 captured fawns were males; of 18 fawn mortalities that could be sexed, 7 were males. Similarly, A. C. Clark (pers. comm.) found a total of 14 males and 12 females among fawns captured or found dead during 1978 on the Refuge. Our approach did not allow us to detect a skewed sex ratio favoring females in 1 year followed by a skewed ratio favoring males the next, but the lack of significance over the 5-year period indicated no consistent trend toward a disproportionate birth of 1 sex. Sex ratio at birth favored males slightly in elk in British Columbia (Cowan 1950), mule deer in Utah (Robinette et al. 1957), and white-tailed deer in Indiana (Kirkpatrick et al. 1976). In a study of penned whitetails, Verme (1969) found that a higher percentage of male fawns were born to does on a low plane of nutrition prior to conception than to does fed better rations.

The sex ratio of yearlings and adults were determined from herd composition counts in autumn-early winter. October-December was the period in which males were best distinguished from females physically. While observability of the sexes was significantly different in only 2 months, September 1974 and October 1975, an analysis of observability of collared bucks and does in 1974 and 1975 indicated that in November, observability of each sex was least dissimilar (Table 8). Sex ratio data collected in November, then, best reflected the actual proportions of each sex in the population. Our analysis was based on herd composition counts and the knowledge of which marked deer were in the population during each count.

The adult-yearling sex ratio in November ranged from 29-42 males per 100 females and was relatively constant from 1972-77 (Table 9). Excluding fawns, there were about 3 females for every male in November during those years (1972-75) when most of the population data were collected. Although sample sizes were an order of magnitude greater in

Table 8. Comparison of observability by month of collared yearling and adult male with collared yearling and adult female white-tailed deer on the CWT National Wildlife Refuge mainland.

	Males			Females			G-value ^d
	Obs. ^a	Exp. ^b	N ^c	Obs. ^a	Exp. ^b	N ^c	
<u>1974</u>							
Sept	9	16.8	5	67	59.2	13	4.666, P<0.05
Oct	32	41.4	6	94	84.6	12	2.964, P>0.05
Nov	31	35.0	7	71	67.0	12	0.531, P>0.10
Dec	47	59.0	7	108	96.0	12	3.732, P>0.05
<u>1975</u>							
Sept	21	24.7	5	73	69.3	15	0.578, P>0.10
Oct	10	26.5	4	116	99.5	15	15.047, P<0.005
Nov	18	18.5	4	98	97.5	18	0.000, P>0.975
Dec	32	29.1	4	162	164.9	17	0.224, P>0.50

^aNumber of times collared deer were observed.

^bExample of how expected value was calculated for males in September 1974: total no. of deer-months that collared males were in September 1974 population (3.47) / total no. of deer-months that collared deer of both sexes were in September 1974 population (15.67) X total no. of observations of collared deer (76) = 16.8.

^cNumber of different collared deer in population.

^dCompares whether observability of collared males is significantly different than observability of collared females. Yates' continuity correction was used in each test with df=1 throughout.

Table 9. Buck:doe:fawn ratios of white-tailed deer on the CWT National Wildlife Refuge mainland.^a

	<u>1972</u>	<u>1974</u>	<u>1975</u>	<u>1976</u>	<u>1977</u>
October	32:100:26 (1613)	32:100:52 (65)	32:100:28 (131)	--	--
November	34:100:35 (1830)	34:100:60 (84)	29:100:37 (170)	38:100:41 (128)	42:100:60 (238)
December	27:100:24 (1445)	21:100:54 (55)	30:100:41 (241)	--	--

^aSample sizes in parentheses.

1972 than any other year, the number of deer classified each subsequent month was still large relative to population size, except in 1974 (see Tables 9-10).

It is not uncommon to find skewed sex ratios favoring females in populations of North American deer. Of course, heavy buck-only hunting could result in such ratios, but the presence of skewed ratios in non-hunted populations deserves greater attention. Hirth (1977) observed a sex ratio of approximately 2 whitetail females per male on Welder Wildlife Refuge. Ratios of approximately 2 females per male were found in several Minnesota whitetail populations, where the population was either expanding or at saturation as evidenced by the overbrowsed condition of the habitat (Gunvalson et al. 1952), and mule deer females outnumbered males 2:1 in Nebraska National Forest prior to hunting (Mohler et al. 1951). Cowan (1950) documented skewed sex ratios favoring females on overstocked range in non-hunted populations of mule deer, elk, caribou (Rangifer arcticus), mountain goat (Oreamnos americanus) and bighorn sheep (Ovis canadensis) in Canada's national parks. He did find that males outnumbered females in moose (Alces americana), however. Numerous researchers have reported sex ratios favoring females in hunted populations of Odocoileus that, purportedly, were not caused by the particular hunting system that population experienced (Klein and Olson 1960, Hirth 1977, Kirkpatrick et al. 1976).

Fawn:doe ratios. Fawn:doe ratios were derived from the same herd composition counts used to calculate sex ratios. Since most fawn mortality occurred during summer (see Mortality), November fawn:doe ratios approximated the number of yearlings that would be recruited into the population the following June. Fawn:doe ratios in November ranged from 35-60 fawns per 100 does (Table 10). The doe category included the yearling age class, so that these ratios reflected the inclusion of females (1.5-year-olds) that did not have fawns of their own, as discussed in the next section. Therefore, the number of fawns per 100 females of reproductive age would be higher than indicated in Table 10.

Table 10. Hypothetical number of white-tailed deer bucks, does and fawns on the CWTN National Wildlife Refuge mainland in November, as derived from population estimates and herd composition data.^a

	<u>Bucks</u>	<u>Does</u>	<u>Fawns</u>	<u>N^b</u>
1972	43 (20)	127 (59)	45 (21)	215
1974	38 (18)	110 (52)	66 (31)	214
1975	31 (18)	108 (60)	40 (22)	180
1976	35 (21)	92 (56)	38 (23)	164
1977	42 (21)	100 (50)	60 (30)	202

^aPercentage of total population in parentheses.

^bPopulation estimate for 1972 was taken as midpoint of Suring's (1974) winter estimate; estimates for 1974-77 were taken from Table 4.

Herd composition. The hypothetical number of bucks, does and fawns in the population was calculated, using November estimates of population size and the sex and age ratios in Table 9 (Table 10). From 1972-77 (no data were available for 1973), composition of this population was relatively constant. The estimated number of yearling and adult males in the November population ranged from 31-43 (18-21%), yearling and adult females ranged from 92-127 (50-60%), and fawns ranged from 38-66 (21-31%).

Summary. The CWTB population on the study area was moderately dense, relative to other whitetail populations, and exhibited a contagious pattern of dispersion. Number of deer observed in each of 3 sections of the Refuge was significantly correlated with percentage of woodland in each of those sections. Apparently, neonatal sex ratio did not differ significantly from 1:1; sex ratio of yearlings plus adults in November of each year remained at about 3 females per male. Although the percentage of the population comprised of females and fawns was more variable than that of males, composition of the herd by sex and age was relatively constant.

Sociality

The nature and duration of social bonds between (or among) individual deer can have an effect on or be affected by other population parameters, such as density, dispersion and dispersal. Because of these potential relationships, we have presented data on CWTB sociality that should increase our understanding of this population's behavior, and be comparable to similar data on white-tailed deer populations elsewhere. It is not intended as a thorough treatment of social organization of CWTB.

Deer that were observed feeding, resting or moving together in relatively close proximity were defined as a social group and could include related as well as non-related individuals. Undoubtedly, our observations of deer included some temporary aggregations of feeding deer that would generally not be considered social groups, but we felt

that samples were large enough to reflect real changes in sociality from month to month.

The format of Tables 11 and 12 were modeled after those for Key Deer to make possible direct comparisons between these 2 races of endangered whitetails. Frequencies of association (FA) between 2 deer were calculated as in Hardin et al. (1976:456), and based on (1) the number of times 2 deer, A and B, were seen together, (2) the number of times deer A was seen without B, and (3) the number of times deer B was seen without A. FA was then calculated as: $FA = [(1)/[(1)+(2)+(3)]] \times 100$, where (1)+(2)+(3) equals the sample size, N.

Group size. The percentage of deer that occurred alone was largest in June (66.4%) and November (53.3%), which corresponded to peaks in fawning and rutting, respectively (Table 11). Adult females generally ceased to associate with their fawns of the previous year in late May-early June, when pregnant does became more solitary and secretive just prior to parturition. FA between marked females and their marked fawns dropped from 47.5 in May to 26.5 in June for female fawns, and from 65.2 to 11.1 for male fawns during the same period (Table 12). Fawns born in June were not regularly observed with the dam until September-October, which raised mean size of groups in late summer-early autumn (Table 11). The rut in November resulted in dissolution of buck groups and temporary separations of does and their fawns, both of which increased observations of single deer. After the November peak in breeding activities, groups containing several does and fawns were common as were social groups of yearling and adult males. Mean group size remained above 2.24 for the rest of the winter until May, when doe-fawn associations began to break. It is important to realize that from June through May of the following year, the size of the population gradually decreased with the death of each individual, so that higher mean size of groups in winter reflected a real tendency toward increased sociality, rather than a response to increased density.

Throughout the year, Key Deer were more solitary than were CWTD. Of 13743 observations of Key Deer groups, 9853 (71.7%) occurred as

Table 11. Size of white-tailed deer groups observed during morning and evening feeding periods on the CWTN National Wildlife Refuge mainland, 1972-73.

Month	\bar{x} (SD)	Number of "groups" that contained ^a									Total no. of groups
		1	2	3	4	5	6	7	8	9+	
July	2.07(1.50)	96(48.2)	51(25.6)	23(11.6)	15(7.5)	7(3.5)	3(1.5)	2(1.0)	1(0.5)	1(0.5)	199
August	2.25(1.55)	370(40.1)	265(28.7)	139(15.1)	70(7.6)	39(4.2)	14(1.5)	17(1.8)	2(0.2)	7(0.8)	923
September	2.54(1.88)	213(32.1)	221(33.3)	96(14.5)	45(6.8)	40(6.0)	25(3.8)	9(1.4)	5(0.8)	10(1.5)	664
October	2.42(1.96)	250(37.5)	205(30.7)	88(13.2)	55(8.2)	32(4.8)	12(1.8)	9(1.3)	3(0.4)	13(1.9)	667
November	1.82(1.24)	537(53.3)	283(28.1)	103(10.2)	49(4.9)	17(1.7)	8(0.8)	4(0.4)	3(0.3)	4(0.4)	1008
December	1.93(1.37)	394(52.7)	180(24.1)	87(11.6)	44(5.9)	23(3.1)	13(1.7)	2(0.3)	2(0.3)	3(0.4)	748
January	2.24(1.69)	386(41.0)	267(28.3)	152(16.1)	66(7.0)	33(3.5)	12(1.3)	10(1.1)	6(0.6)	10(1.1)	942
February	2.50(2.18)	222(39.6)	156(27.9)	72(12.9)	40(7.1)	28(5.0)	16(2.9)	7(1.2)	6(1.1)	13(2.3)	560
March	2.49(1.83)	223(35.6)	182(29.0)	90(14.4)	60(9.6)	31(4.9)	16(2.6)	12(1.9)	2(0.3)	11(1.8)	627
April	2.39(1.85)	255(38.5)	185(27.9)	114(17.2)	47(7.1)	17(2.6)	17(2.6)	7(1.1)	5(0.8)	15(2.3)	662
May	1.90(1.18)	333(46.5)	229(32.0)	93(13.0)	37(5.2)	11(1.5)	9(1.3)	1(0.1)	2(0.3)	1(0.1)	716
June	1.54(0.97)	340(66.4)	107(20.9)	37(7.2)	21(4.1)	4(0.8)	2(0.4)	0(0.0)	0(0.0)	1(0.2)	512
Total		3619(44.0)	2331(28.3)	1094(13.3)	549(6.7)	282(3.4)	147(1.8)	80(1.0)	37(0.4)	84(1.0)	8228

^aPercentage of all groups observed that month in parentheses.

Table 12. Frequencies of association (FA) between marked does and their marked fawns on the CWT National Wildlife Refuge mainland.^a

<u>ADULT DOE-FEMALE FAWN</u>					<u>ADULT DOE-MALE FAWN</u>				
<u>No. of pairs</u>	<u>FA (mean)^b</u>	<u>N</u>	<u>Range</u>	<u>Month</u>	<u>No. of pairs</u>	<u>FA (mean)^b</u>	<u>N</u>	<u>Range</u>	
--	--	--	--	Jun	4	8.3	24	0.0-40.0	
--	--	--	--	Jul	4	19.0	20	0.0-25.0	
--	--	--	--	Aug	3	17.6	17	0.0-50.0	
--	--	--	--	Sept	3	31.6	19	0.0-100.0	
--	--	--	--	Oct	2	46.4	28	28.6-74.3	
--	--	--	--	Nov	4	38.9	36	14.3-100.0	
--	--	--	--	Dec	4	76.6	47	75.0-100.0	
2	33.3	6	0.0-40.0	Jan	3	79.5	39	60.0-90.0	
3	58.8	34	50.0-75.0	Feb	4	80.4	46	33.3-83.3	
3	66.7	39	50.0-82.4	Mar	4	90.9	33	50.0-100.0	
3	50.8	65	25.0-77.3	Apr	4	89.8	99	83.3-100.0	
4	47.5	40	0.0-87.5	May	4	65.2	23	45.5-100.0	
4	26.5	34	0.0-34.8	Jun ^c	3	11.1	27	0.0-25.0	
2	0.0	9	0.0	Jul ^c	2	0.0	8	0.0	
1	0.0	9	0.0	Aug ^c	2	10.0	10	0.0-33.3	

^aFA was based on (1) no. of times 2 deer, A and B, were seen together, (2) no. of times deer A was seen without B, and (3) no. of times deer B was seen without A. $FA = [(1)/[(1)+(2)+(3)]] \times 100$, where (1)+(2)+(3) equals the sample size, N.

^bWeighted averages were used to account for differences in sample sizes.

^cThese actually consisted of doe-yearling pairs, since fawns were advanced to the yearling age class on 1 June.

single deer, whereas 3890 (28.3%) were of groups of 2 or more (Hardin et al. 1976:456). Of a total of 8228 observations of CWTB groups, 3619 (44.0%) and 4609 (56.0%) occurred as singles and groups of 2 or more, respectively. FA between Key Deer and their fawns were comparable to those of CWTB prior to fawns reaching 7 months of age, although we had data only for does and their male fawns of this age. After fawns were 7 months of age or older, FA between dams and female fawns averaged 37.0 for Key Deer; for dams and male fawns it averaged 40.4 (Hardin et al. 1976:459). For fawns of the same age, FA for CWTB averaged 52.9 and 75.8 for dam-female fawns and dam-male fawns, respectively. Hawkins and Klimstra (1970:410) obtained FA for white-tailed deer in Illinois that averaged 72 for doe-female fawns and 75 for doe-male fawns during a comparable period of fawn age. Hawkins and Klimstra calculated FA in a manner that resulted in slightly lower estimates than the formula used for Key Deer and Columbian whitetails (J. W. Hardin, pers. comm.).

Buck groups. We recorded the location, size and age composition of all groups containing 3 or more yearling or adult males (i.e., buck groups) that were observed from February 1975-March 1976 (Table 13). Based on the actual number of buck groups observed by month, we concluded that CWTB males were least social during late summer and autumn on the Refuge. A mean of 3.3 buck groups per month was observed during August-November, while a mean of 14.9 buck groups per month was observed during December-May. Mean size of buck groups during August-November (3.3) as compared to December-May (4.1) also reflected a decrease in sociality among males in late summer. Although observability of all deer was lower during summer due to denser vegetation, this bias was probably compensated (partially) during winter by the difficulty of identifying males at a distance after antler-drop. The period of decreased sociality occurred at that time of year when males had developing antlers covered with sensitive, vascular tissue or were actively engaged in rutting activities. At least 70.5% of all males observed in buck groups were adults; a minimum of 7.5% were yearlings. The largest buck group was

Table 13. Description and frequency of all-male social groups of white-tailed deer observed from February 1975-March 1976 on the CWT National Wildlife Refuge mainland.^a

	No. of groups	No. of males	GROUP SIZE		COMPOSITION		
			Mean (SD)	Range	Adults	Year.	Unk. ^b
<u>1975</u>							
Feb	16	88	5.5 (1.8)	3-9	56	8	24
Mar	9	38	4.2 (1.1)	3-6	25	2	11
Apr	26	101	3.9 (1.1)	3-7	60	3	38
May	15	59	3.9 (1.3)	3-8	18	1	40
Jun	13	45	3.5 (0.7)	3-5	41	0	4
Jul	12	45	3.8 (1.1)	3-6	43	1	1
Aug	4	12	3.0 (0.0)	3	10	2	0
Sept	4	14	3.5 (1.0)	3-5	10	4	0
Oct	4	13	3.3 (0.5)	3-4	11	2	0
Nov	1	4	4.0 (0.0)	4	3	1	0
Dec	12	47	3.9 (1.4)	3-7	34	10	3
<u>1976</u>							
Jan	21	82	3.9 (1.1)	3-7	66	10	6
Feb	11	47	4.3 (1.0)	3-6	40	3	4
Mar ^c	<u>14</u>	<u>56</u>	<u>4.0 (0.8)</u>	<u>3-5</u>	<u>42</u>	<u>2</u>	<u>12</u>
Total	162	651	4.0 (1.2)	3-9	459	49	143

^aNumber of all-male groups (i.e., groups with 3 or more males) observed from January-March and June-August was probably conservative due to antler-drop and poor visibility caused by dense vegetation, respectively.

^bMales whose age could not be determined with certainty.

^cObservations ended on 15 March 1976.

observed in February 1975 and contained 9 males.

The area of the Refuge of greatest concentration of buck groups during 1974-76, based on absolute number of observations of such groups, was shown earlier (Fig. 7). Many groups were observed more than once as evidenced by the presence of marked males, but these groups appeared to be very loose in structure, with frequent exchange of members among groups. This pattern of concentration of males at the western end of the Refuge, then, related more to heavy use of a preferred area by a relatively small number of males, than to dense concentrations of a large number of different males. It is interesting that the pattern of male dispersal depicted in Fig. 16, showed a net movement with increasing age by each of the 7 males toward this area that was apparently preferred by males.

In Texas, Brown (1974:437) found that core membership in groups of whitetail males usually consisted of 2-4 animals, but that the strongest attachments were between pairs of males. On the CWTDNWR, 2 adult males (Nos. 60 and 38), who were not observed together until after the rut in 1974, had a FA of 20.8 (N = 96) from December until No. 60 lost his collar the following May. However, both males were regularly observed in buck groups without the other during this period.

Summary. The percentage of all observations of CWTD that consisted of single deer was largest in June (fawning) and November (rut). Frequencies of association between marked females and their marked fawns dropped abruptly from May to June, when fawns became 1 year old and females approached parturition. Key Deer were generally more solitary than CWTD and had lower frequencies of association between does and their fawns after fawns reached 7 months of age than did CWTD. Buck groups, which were mainly composed of adult males, were more commonly observed during winter-spring than late summer-autumn and were observed most often at the western end of the Refuge.

Reproduction

It would have been valuable to document the number of young deer per adult female that attained age of independence each year. This is a reasonable definition of recruitment rate; it would have required an accurate measurement of the number of fawns per doe prior to their separation near the fawn's 1st birthday. This was virtually impossible due to low observability of females at that time of year and increased difficulty in distinguishing large fawns (usually males) from some older deer. Public and legal aspects of working with an endangered species and a desire not to unduly perturb this population, precluded collection of females prior to parturition to determine fecundity rates. We knew that neonatal mortality was substantial, but mortality was very low after fawns reached 3-5 months of age. As explained earlier, November was the best month to determine sex and age ratios in the population and, given the fawn mortality pattern, was the best period to use in comparing reproductive (= fawning) success among years. Since mortality of fawns from November to the following June was low, a measurement of fawning success in November liberally approximated recruitment rate, which we could not directly document. The term "recruitment rate" will be used hereafter to apply to this measurement.

Pregnancy and fecundity. Based on the approximate age of captured fawns and those found dead, and the behavior of females, parturition was concentrated in early to mid-June. No fawn was captured prior to 9 June in 1975 or 1976 or before 12 June in 1973; females appeared to be pregnant until after 1 June in 1975 and 1976. Some fawning did occur throughout the summer, however; at least 2 females gave birth as late as October.

We observed marked females 2-3 weeks prior to parturition in 1975 and 1976 to document visible pregnancies. Visible signs of pregnancy (i.e., distended abdomens), along with observations of whether these same marked females were accompanied by fawns at any time after parturition, were used to calculate the percentage of marked females pregnant. Percentages for females \geq 3 years old, 2 years old and 1 year old (ages in June) were 100, 70 and 0, based on a total sample size for both

years of 20, 10 and 5, respectively. The estimate of pregnancy rate among 2-year-old females may have been conservative, since visible signs of pregnancy were not as evident as in older and larger females. Throughout this study, there was no indication that marked or unmarked female fawns ever participated in breeding, and subsequently, no yearling female was ever observed with a fawn we thought belonged to her.

Two adult females that were illegally shot in February 1975 and 1 adult female found dead in January 1976 were pregnant with twins. The ovaries from 1 additional female carcass recovered in November contained 2 corpora lutea of pregnancy. These were the only adult females obtained in suitable condition during the time they should be pregnant (November-June). In addition, a marked female (#17) was observed in June 1975 within 1 hour after parturition; she had given birth to twins. These data were few ($N = 5$), but suggested that adult females on the Refuge generally carried 2 fetuses and dropped 2 fawns in June. Additional observations of sets of twins during summer supported this conclusion. In other whitetail populations, mean number of embryos per adult doe prior to fawning were 1.85 in New York (O'Pezio 1978), 1.94 in Indiana (Kirkpatrick et al. 1976), 1.89-1.92 in 3 areas in Manitoba (Ransom 1967) and 1.93 in Illinois (Roseberry and Klimstra 1970). A collection of 12 females yielded 24 fetuses in Montana (Allen 1968).

Recruitment rates and inversivity. To estimate recruitment rates, we observed marked females intensively to determine their fawning success in November, and used these rates to interpret fawn:doe ratios calculated for the entire herd. Validity of these estimates assumed that adoption of orphaned fawns by marked females was rare or non-existent. Our sample of intensively observed females represented 59 doe-years, a 14% sample of all females that were hypothetically in the November populations of 1974-77 (from Table 10).

Recruitment rate was highest for females ≥ 3.5 years old (0.75-0.85), lower for 2.5-year-olds (0.36), while 1.5-year-olds made no contribution (0.00) (Table 14). The small expected value for the

Table 14. Recruitment and twinning rates of marked white-tailed deer females on the CWTN National Wildlife Refuge mainland, as measured in November 1974-77.

	Age of does in years		
	<u>1.5</u>	<u>2.5</u>	<u>≥3.5</u>
Doe-years ^a	8	11	40
No. of fawns	0	4	30-34 ^b
Recruitment rate ^c (fawns/doe)	0.00	0.36	0.75-0.85
Twins in November (sets/doe)	0.00	0.00	0.15-0.18

^aOnly females marked prior to 1 June were included in that year's calculations to eliminate capture bias due to presence or absence of fawns.

^bIt was not certain whether several fawns observed with marked does actually belonged to those females. The midpoint of this range (32) was used in statistical tests.

^cRate of 2.5-year old females was not significantly different than females ≥3.5 years old ($G=2.021$, $df=1$, $P>0.10$). Recruitment rate of yearling females not tested due to low expected frequency.

1.5-year-old age class prevented statistical testing among all 3 age classes, and the difference in recruitment rates between 2.5-year-olds and females ≥ 3.5 years old was not significant ($P > 0.10$). Only 6 or 7 sets of twins belonging to marked females were known to survive until November and they were always associated with females ≥ 3.5 years old. Five of these sets were recorded in November 1977, while 1 set was observed in 1974 and 1 in 1976. It was not definitely known whether this latter pair actually consisted of 2 fawns born to the same doe. The twinning rates in Table 14 should be referred to as twin survival rates, since they related the number of sets of twins alive in November, rather than the number born in June, to the number of females.

There was neither a significant difference in recruitment rate among the years 1974-77 ($P > 0.10$) nor between 1975 and the other years ($P > 0.05$), although the rate was lowest in 1975 (Table 15). In all comparisons that involved recruitment rates from Table 15, mean values in 1976 and 1977 (i.e., 0.85 and 1.04, respectively) were considered most reasonable to use. The range in recruitment rates for these years was due to the uncertainty of establishing fawning success for some does. Stormer (1972, in Kirkpatrick et al. 1976), in analyzing natality rates rather than recruitment rates, found significant differences among fawn, yearling and adult females, but no difference in natality rates among years within those age classes. He studied a population of white-tails in Indiana where female fawns had a conception rate of 20%.

We do not know what determined recruitment rate among adult females in any given year, but there was a significant inverse correlation between recruitment rates of marked females (≥ 3.5 years old) and the population estimate for November of the previous year ($r = -0.998$, $P < 0.05$). This relationship between density and reproductive success, if it holds, could provide the negative feedback mechanism to account for the observed stability in population size. By definition, such a system would be considered regulated (Sinclair 1974:135). We could only theorize as to the exact nature of such a mechanism, but data presented in the next section (Mortality) substantiated that it was the magnitude of fawn mortality, not fecundity, that determined recruitment rate in

Table 15. Recruitment rate by year among marked white-tailed deer females on the CWT National Wildlife Refuge mainland, as measured in November.^a

	FEMALES ≥ 3.5 YEARS OLD			FEMALES ≥ 2.5 YEARS OLD		
	<u>No. of females^b</u>	<u>No. of fawns</u>	<u>Fawns/doe^c</u>	<u>No. of females^b</u>	<u>No. of fawns</u>	<u>Fawns/doe^c</u>
1974	7	6	0.86	8	7	0.88
1975	9	3	0.33	12	4	0.33
1976	10	8-9	0.80-0.90	17	10-11	0.59-0.65
1977	<u>14</u>	<u>13-16</u>	<u>0.93-1.14</u>	<u>14</u>	<u>13-16</u>	<u>0.93-1.14</u>
Total	40	30-34	0.75-0.85	51	34-38	0.67-0.75

^aNo significant difference in recruitment rate among years for females ≥ 3.5 years old ($G=4.095$, $df=3$, $P>0.10$) or when including females 2.5 years old ($G=5.356$, $df=3$, $P>0.10$).

^bOnly females marked prior to 1 June and observed often enough to determine number of fawns at heel were included.

^cMidpoint of ranges used in statistical tests.

any given year.

Pattern of reproduction. The causal relationship between the physical condition of a female mammal and her productivity is generally accepted (Vaughan 1972:284). In white-tailed deer, Verme (1969) found that a low plane of nutrition prior to breeding resulted in reduced fertility and that those does who lost fawns to mortality were more productive the following year. He attributed this to the ability of the female to regain good physical condition after early release from the stress of lactation that would normally reduce fertility during the breeding season in autumn somewhat proportionally to the number of fawns that she raised earlier that summer (Verme 1967:416).

Our limited data on reproductive success of 14 marked, CWTD females ≥ 2.5 years old did not substantiate such a trend in this population (Table 16). Although the mean number of fawns per doe in November was 0.90-1.0 (9-10 fawns per 10 doe-years) for adult females in years following one of zero recruitment and 0.83 (15 fawns per 18 doe-years) for females following a successful year, this was not a significant difference ($G = 0.011$, $df = 1$, $P > 0.90$). After deleting 2.5-year-old females from the sample, comparable means were 0.71-0.86 (5-6 fawns per 7 doe-years) and 0.80 (12 fawns per 15 doe-years) for females in years following no recruitment and successful recruitment, respectively. The inclusion of 2.5-year-old females in the sample would explain the different trend found between samples, since these females were less successful than older females in recruiting fawns (Table 14), but were usually successful as 3.5-year-olds.

Interpretation of fawn:doe ratios. The difference in fawning success among female age classes made interpretation of fawn:doe ratios difficult, since data from herd composition counts did not distinguish among age classes of females. Since we did not know what proportion of females belonged to each age class in November, a low fawn:doe ratio may have indicated poor fawning success among females ≥ 3.5 years old, or, good success for these older females with a high proportion of yearling females in the November population, or any number of

Table 16. Number of fawns successfully raised to November by collared white-tailed deer females on the CWTN National Wildlife Refuge mainland.

Collar # ^a	Age of female in 1974	NUMBER OF FAWNS			
		1974	1975	1976	1977
31	≥4.5	0	1	1	0
17	2.5	1	0	1	0
7	≥3.5	0	0	1	2
27	≥3.5	1	0	1-2	2
23	≥2.5	1	1	0	1
52	1.5	0	1	1	2
59	1.5	0	0	1	1
A4	4.5	--	1	0	0
A3	≥1.5	--	1	1	1
1	3.5	1	1	--	--
5	≥3.5	1	0	--	--
54	1.5	0	0	1	--
53	0.5	--	0	0	2
28	0.5	--	0	1	2

^aOnly females were included whose reproductive success was known with virtual certainty in 2 consecutive years as an adult (i.e., at least 2.5 years old).

intermediate combinations of recruitment rates and proportions of various-aged females. If we assume that the fawning success of the cohort of marked females ≥ 3.5 years old was truly representative of all females in the population of that age, then the resultant correlation coefficient between the annual recruitment rates for marked females (≥ 3.5 years old) and for all females for the years 1974-77 ($r = 0.763$, $P > 0.05$), indicated that fawn:doe ratios were greatly influenced by the proportion of younger deer in the female cohort. Fawn:doe ratios for this population, then, were of little value in comparing reproductive success of females among years, but could be used in conjunction with a population estimate and sex ratio information to calculate the proportion of the population comprised of fawns (Table 10) and, subsequently, as a gross predictor of the number of yearling deer in next year's population.

Summary. Available data indicated that most adult females in this population became pregnant, usually with twins, and gave birth during June. Females apparently gave birth for the first time at 2 years of age, but were less successful in producing and/or raising fawns than were older females. Sets of twins were uncommon by autumn. The number of fawns per marked female in November did not differ significantly among years, but there was an inverse relationship between fawning success of females ≥ 3.5 years old (in November) and the population estimate for the previous November. There was no discernible pattern among adult females that suggested that success in raising fawns in one year had any effect on the following year's success. Correlation analysis revealed that fawn:doe ratios based on herd composition counts in autumn were significantly influenced by the proportion of young females in the population and were, therefore, not a reliable indication of fawning success among adult females.

Mortality

Temporal distribution by sex and age. The location of dead deer found on the Refuge and an estimate of the month of death were used to compare

the timing of mortality by sex and age. All mortalities that occurred from June 1974-December 1977, except those due to capture attempts and poaching, were included in this analysis (Table 17). Road-killed deer were included since this form of mortality probably reflected seasonal changes in deer behavior that predisposed them to this mortality factor (e.g., rutting in males). Known road kills accounted for only 9 of 137 mortalities used in this analysis.

To compare the magnitude of mortality within any sex or age class for 2 different time periods would have required a major assumption: the ability to locate carcasses of that sex or age class was equal between those time periods. Factors influencing the ability to locate carcasses included the time spent searching, seasonal changes in vegetation, presence or absence of turkey vultures, carcass size (fawns) and rate of carcass decomposition. We chose not to make the assumption of equal recovery rate of carcasses through time and avoided quantitative comparisons between time periods within a sex or age class. It was obvious, however, that the heaviest fawn mortality must have occurred from June-August, as 77% of all fawn carcasses that were located were estimated to have died during the period (summer) when carcasses were most difficult to find, decomposed the fastest, and fawns were the smallest. The same temporal pattern of fawn mortality for whitetails was found in south Texas (Cook et al. 1971).

In comparing the mortality pattern between sex and age classes within the same time period, we assumed it was no easier to find the carcass of one sex or age class than another. This assumption was probably met with regard to all classes except fawns; deer less than 1 year old were excluded from the analysis for this reason. Since yearling males displayed the same temporal mortality pattern as adult males and yearling females the same as adult females, these age classes were combined to examine male versus female mortality.

We chose to divide the year into 2 6-month periods: May-October represented that time when females were experiencing the stress of late gestation, fawning and lactation; November-April can be referred to as the rutting/post-rutting period. The variables associated with the

Table 17. Temporal distribution of natural mortalities (plus road kills) of white-tailed deer on the CWTD National Wildlife Refuge mainland, June 1974-December 1977.

	NOVEMBER-APRIL		MAY-OCTOBER	
	<u>Nov-Jan</u>	<u>Feb-Apr</u>	<u>May-Jul</u>	<u>Aug-Oct</u>
Fawns N=53	6	3	36 ^a	8
Adult males N=36	16	8	4	8
Yearling males N=14	6	5	2	1
Adult females N=30	6	3	8	13
Yearling females N=4	<u>0</u>	<u>1</u>	<u>1</u>	<u>2</u>
Total (N=137)	34	20	51	32

^aNo fawn mortalities were found in May.

search for carcasses were thought to be relatively constant within each of these 6-month periods. The observed ratio of males to females that died within a period was tested against the expected sex ratio obtained from herd composition counts in autumn (i.e., 3 females per male) (Table 9). The number of males (15) that died during May-October relative to females (24) was not different than expected ($G = 2.826$, $df = 1$, $P > 0.05$); the ratio of males to females (35:10) that died during November-April departed significantly from the expected ratio ($G = 52.801$, $df = 1$, $P < 0.005$). That is, from November-April one would expect about 3 times as many females dying as males, if each sex died in proportion to its abundance in the population. What we found, however, indicated that about 3 times as many males died as females.

Spatial distribution of mortalities. The location of each mortality found on the study area was mapped. Since the census data indicated a reduction in deer density in the center of the Refuge (unit R4) from 1974-75 to 1975-76, we applied the data on spatial distribution of mortalities to an understanding of this reduction in density.

Unit R4 (106 ha, 13.4% of the Refuge mainland) was bounded by a series of sloughs and drainage ditches that effectively created a natural unit within the total study area (Fig. 3). Deer did move into and out of the area, but the majority of deer found in R4, especially females, seemed to have rather permanent home ranges within its boundaries. This was substantiated by observations of 7 collared females in this unit. Based on 14 evening censuses of this area from October-March 1974-75 and 20 censuses from October-March 1975-76, the mean number of deer observed per census decreased from 35.4 (SD = 11.4) to 22.8 (SD = 9.0). Similarly, 12 spotlight counts of the same area resulted in a mean of 50.1 (SD = 9.3) deer observed per count in 1974-75 and 27.8 (SD = 7.3) in 1975-76. Although no censuses were conducted in the winter of 1973-74, a mean number of 38.1 deer was observed per census in R4 during October-March 1972-73. This was very close to the mean for 1974-75 and suggested that deer numbers in R4 were relatively constant from 1972-73 to 1974-75. Therefore, the observed

decrease occurred after March 1975.

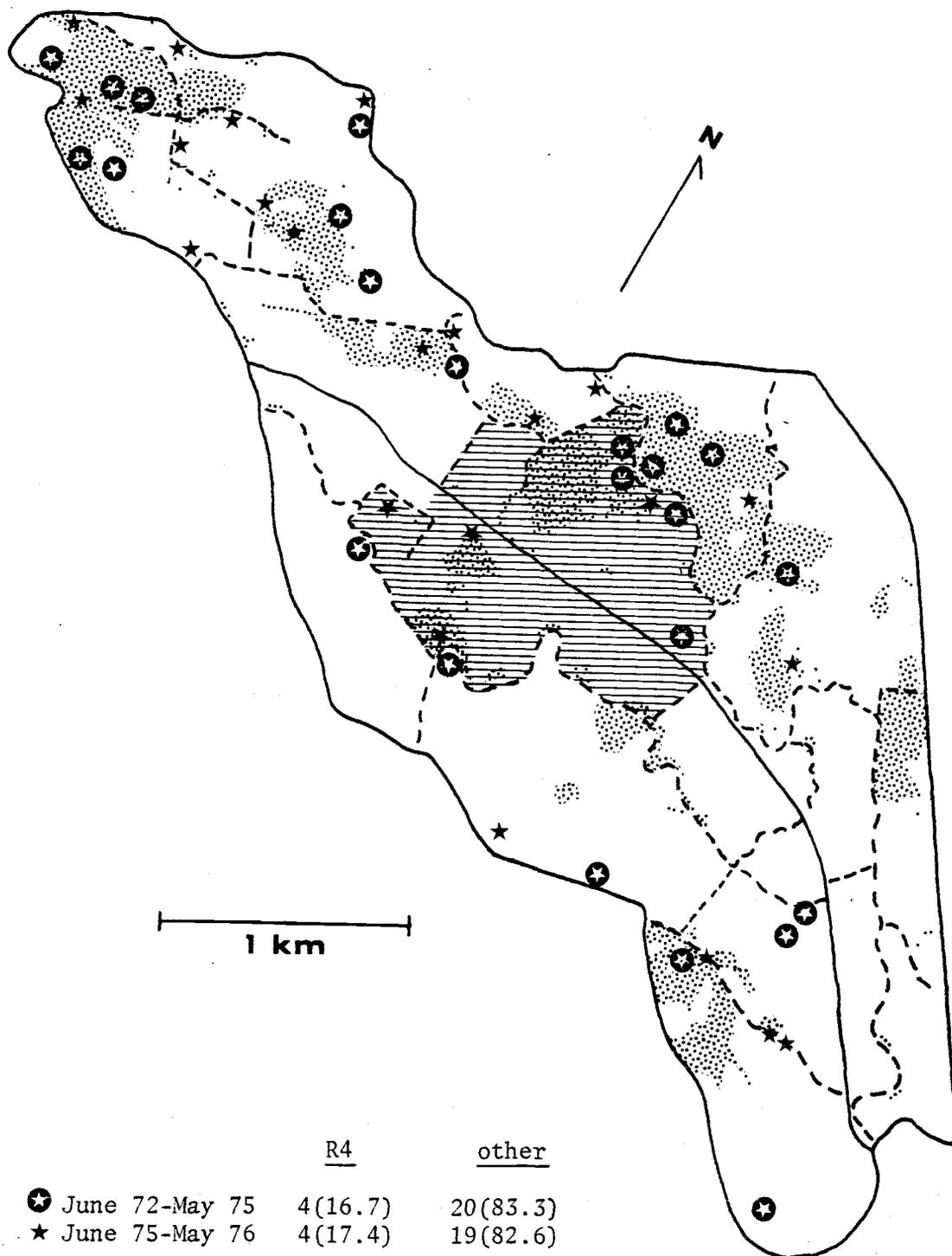
The spatial distribution of CWTD male, female and fawn mortalities (natural) are shown in Figs. 9-11. We compared the proportion of all mortalities of a given sex and age class that was found in unit R4 from June 1972-May 1975 to the proportion found in R4 during June 1975-May 1976. The proportion of neither male nor fawn carcasses recovered from R4 differed significantly between the 2 periods (Figs. 9 and 11). The proportion of female carcasses found in R4 increased dramatically from 23.7% (9 of 38) of all female mortalities in 1972-75 to 84.6% (11 of 13) in 1975-76 ($P < 0.005$).

The reduction in deer density in R4 and concomitant increase in female mortality both occurred during the year when forage in this unit appeared to be low in both quality and quantity. The summer of 1975 was the 3rd consecutive year that cattle were excluded from unit R4 and the hayfield (14.6 ha) in R4 received only 1 cutting. By late summer, grasses in the unit were tall and rank and dense patches of Canada thistle were common; throughout the winter of 1975-76 this unpalatable vegetation formed a large portion of the total plant biomass. This aspect was especially conspicuous from late summer through winter from an observation tower located in the unit; the brown ground cover of dead vegetation in R4 was in marked contrast to the bright green mat of shorter, herbaceous vegetation growing in adjacent units of the Refuge.

To state that females were more adversely affected by the apparent decrease in habitat quality in R4 than were males or fawns deserves clarification. Obviously, sampling intensity over the study area could have influenced the difference in percentage of female carcasses located in R4. The fact that 37 male and fawn carcasses were found outside of R4 in 1975-76, where only 2 females were found, attested to the intensity of our search efforts outside of this unit. In addition, since these proportions were simply relative measures of mortality intensity, inside R4 relative to outside, the high proportion of females found dead in R4 in 1975-76 could have been due to low mortality of females outside of that unit, rather than high mortality inside. At any rate, the high proportion of total female mortalities on such a small area

Figure 9. Spatial distribution of yearling and adult white-tailed deer male mortalities relative to unit R4 on the CWTD National Wildlife Refuge mainland. (Percentage of mortalities for that time period in parentheses).

MALES



$G=0.104$, $df=1$, $P>0.500$

Figure 10. Spatial distribution of yearling and adult white-tailed deer female mortalities relative to unit R4 on the CNTD National Wildlife Refuge mainland. (Percentage of mortalities for that time period in parentheses).

FEMALES

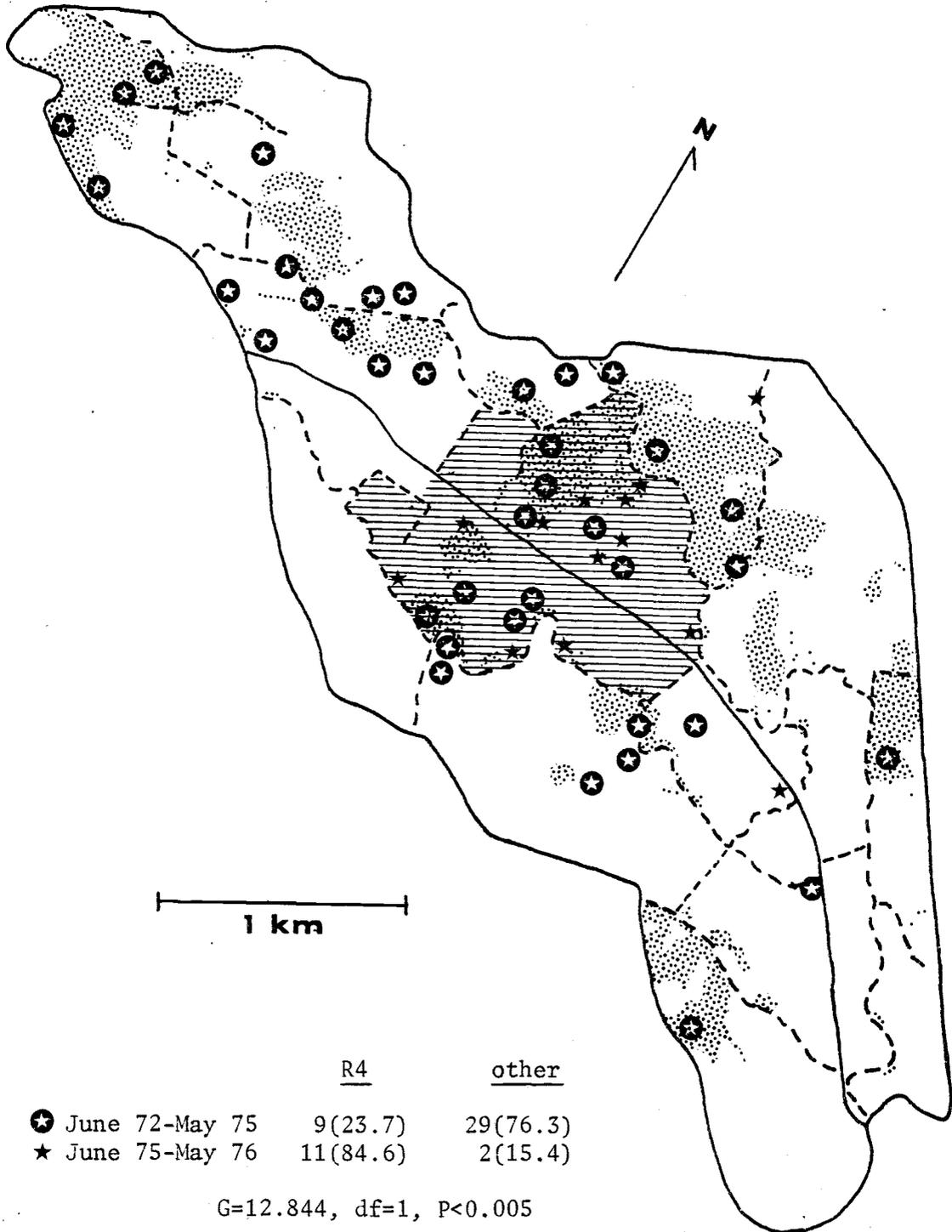
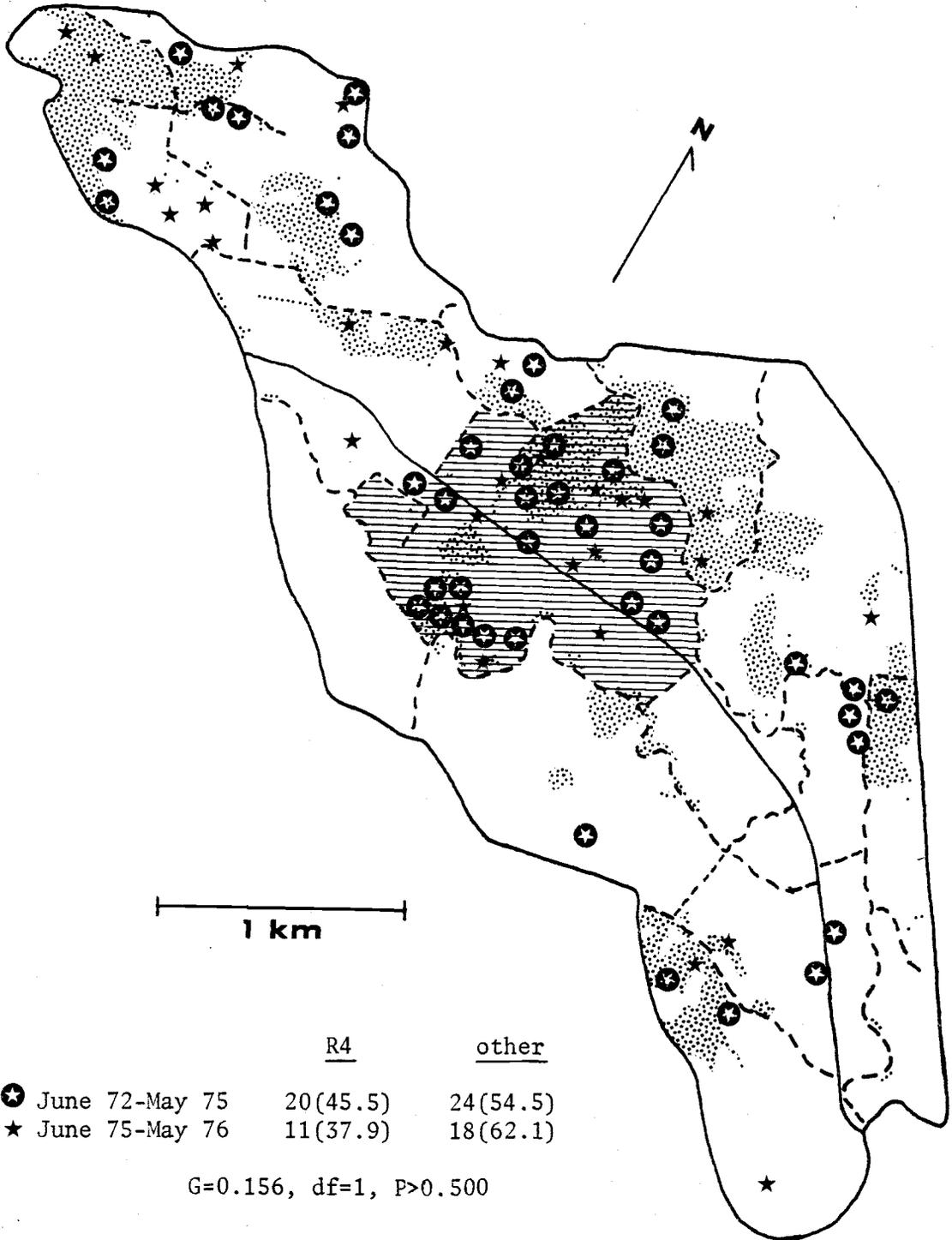


Figure 11. Spatial distribution of white-tailed deer fawn mortalities relative to unit R4 on the CWTN National Wildlife Refuge mainland. (Percentage of mortalities for that time period in parentheses).

FAWNS



(84.6% on 13.4% of the study area) concomitant with what we felt was a degradation of forage quality, suggested a causal relationship. Of 11 female mortalities found in R4 in 1975-76, 10 were adults. Six of these died during June-October, 1 in November, 2 during winter (1 of which drowned), and 1 the following spring.

Age structure. We compared male and female ages at death in this population by constructing separate ecological longevity curves for males (N = 61) and females (N = 60) based on our sample of aged skulls. The construction and interpretation of ecological longevity curves were described by Dapson (1971, 1972), who used them to compare demographic characteristics among populations of Peromyscus polionotus. To our knowledge, this is the first use of this method to compare age structure of males and females within the same population. Since both sexes in this population were exposed to exactly the same environmental conditions, this comparison should reflect ecological, behavioral and/or genetic differences between males and females.

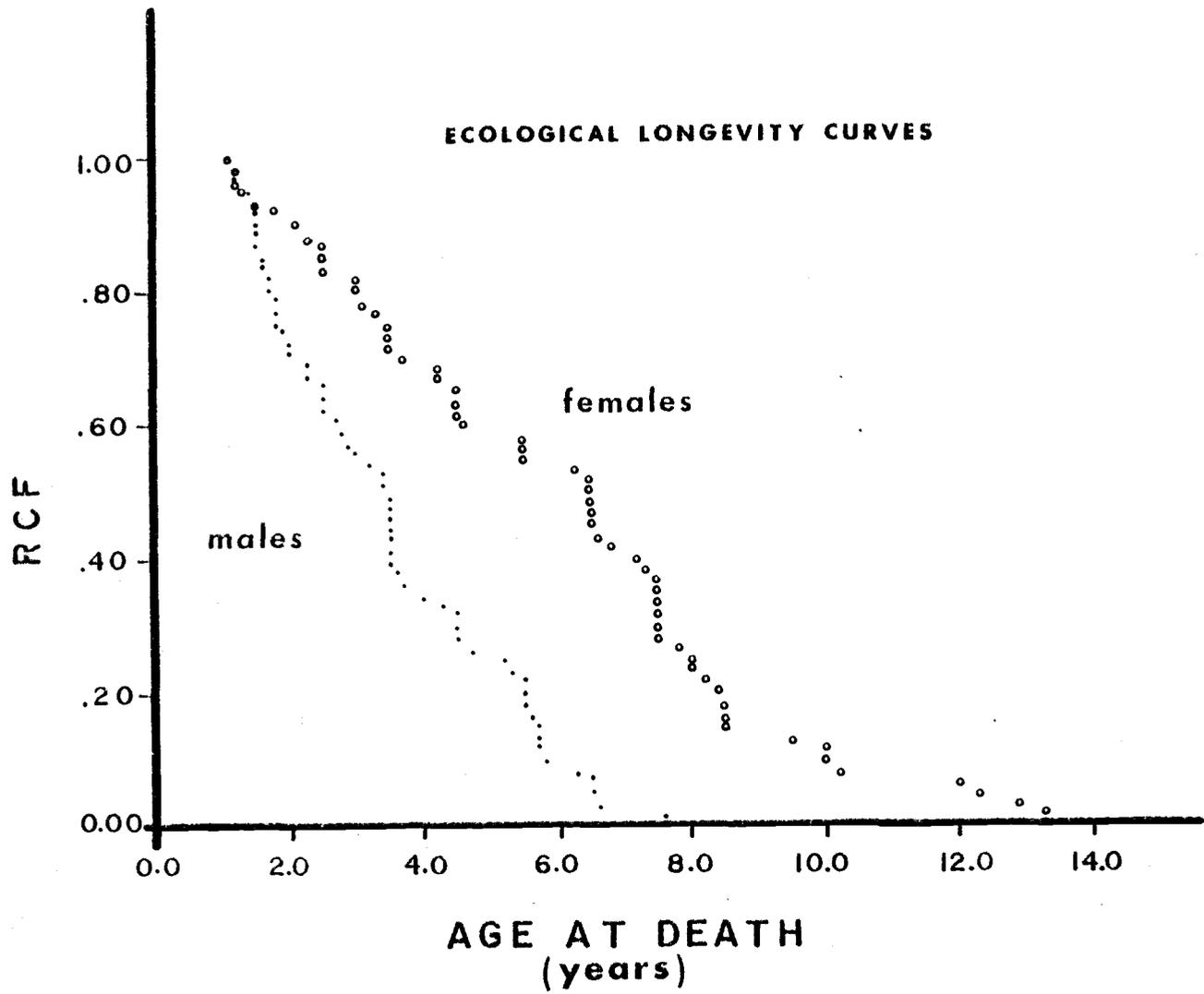
We utilized only deer that died from natural causes, including road kills, and were ≥ 1 year old, due to the bias inherent in finding fawn carcasses relative to older and larger deer. This resulted in a truncated distribution of ages at death. Most skulls were collected during a 2-year period (1974-76), but the total sample included skulls found from June 1972-December 1977. This sample, then, was not a "continuous sample" (Dapson 1971:77), which was defined as one collected over a period of time so that a single cohort could be followed from birth to death, since maximum longevity for each sex was longer than 5 years. In the continuous case, the Y-axis (of the resulting curve) represents probability of survival, rather than probability of occurrence as when an instantaneous sample is used. Since our sample can only be considered nearly continuous, and therefore not truly representative of survivorship, we constructed ecological longevity curves mainly to illustrate the relationship between male and female ages at death. This comparison was further described by 2 parameters: median ecological longevity (MEL) and maximum ecological longevity (MAX). MEL is that age

before which half the population dies (i.e., in our sample, half of those deer that reach 1 year of age die before MEL); half survive beyond MEL. MAX is the greatest age attainable under existing ecological conditions.

To begin, we ordered the ages of each sex from oldest to youngest. The relative cumulative frequency (RCF) was calculated for each of these ages by the formula $1/N$, and accumulated for each subsequent age (Appendix C). The same procedure was applied to males and females. RCF was then plotted on the Y-axis against age on the X-axis and the equation of the line determined. Dapson (1972:163) gives several reasons why age should be treated as the dependent variable, but graphed on the X-axis for ease in graphical interpretation; the dependent variable is usually placed on the Y-axis in conventional regression analysis. We experimented with 8 different models before settling on a "best" model based on the following criterion: the model having the highest coefficient of determination (r^2) and a MAX that approximated, but was larger than, the oldest animal of that sex in the sample. Transformations of 1 or both axes were necessary to obtain an adequate fit to the line. Fortunately, the same transformation resulted in the best model for males and females based on the above criterion. The following equations and associated information were derived for each sex: $(1/\sqrt[4]{X}) = 0.588 + 0.347Y$, $r^2 = 97.6$, MEL = 2.97, MAX = 8.37 for males and $(1/\sqrt[4]{X}) = 0.489 + 0.368Y$, $r^2 = 86.8$, MEL = 4.87, MAX = 17.49 for females (Fig. 12). MEL and MAX can be read directly from Fig. 12, or more accurately determined by solving the regression equation for $Y = 0.5$ and $Y = 0.0$, respectively. Based on counts of cementum annuli, the oldest male in the sample was 7.6 years old at death; the oldest age at death for a female was 13.3 years.

It was apparent that median age at death and maximum ecological longevity were greater for females than males. We compared the medians using a non-parametric test (Zar 1974:114), and found that median age at death was significantly greater for females than males ($G = 13.012$, $df = 1$, $P < 0.005$). Since no assumption need be made regarding age distribution or rate of population increase with this analysis, we can

Figure 12. Ecological longevity curves for Columbian white-tailed deer males and females. (RCF = relative cumulative frequency).



not distinguish the interaction of birth and death processes that result in a given age structure, without additional information.

Mortality rates. Our earlier conclusion that the sex ratio of neonates was 1:1 and the absence of differential mortality by sex among fawns supports the assumption that the sex ratio at 1 year of age did not differ from unity. (Taber and Dasmann (1954) did find higher mortality of male black-tailed deer fawns than female fawns). This suggests that higher mortality of yearling and adult males accounted for the lower ecological longevity in that sex. To estimate mortality rates, we constructed a life table from d_x data (i.e., the same picked-up sample of skulls from natural mortalities in an unexploited population) and utilized the survival column (l_x) to calculate weighted mean mortality rates (\bar{q}) for males and females using the formula:

$$\bar{q} = 1/\sum l_x, \text{ (Caughley 1977:104).} \quad \text{Equation 11}$$

This assumed a population with zero rate of increase (stationary), which November population estimates generally supported.

Emphasis was not placed on interpretation of mortality rates by age class, because samples of males ($N = 61$) and females ($N = 60$) were relatively small. In fact, Caughley (1977:95) stated that a life table approach was inappropriate for a sample less than 150. Fawns were excluded from the analysis due to the bias previously discussed. The omission of the 0-1 age class from the life table resulted in calculation of pooled mortality rates that applied only to deer ≥ 1 year old. The l_x , d_x and q_x columns were included in Table 18 to show how we derived \bar{q} and to present provisional estimates of mortality for each age class.

The pooled annual mortality rate for males (0.345) was nearly twice as high as for females (0.179); that is, from the birth period in one year to the birth period the next, approximately 35% of all yearling and adult males and 18% of all yearling and adult females died. This disproportionate mortality of males not only accounts for the younger age distribution at death for this sex but also, since movement of deer off or onto the Refuge did not occur (see Home Range and Movements), the

Table 18. Life table analysis to derive mortality rates for male (M)^a and female (F) white-tailed deer, excluding fawns, on the CWTD National Wildlife Refuge mainland.

AGE IN YEARS (x)	FOUND DEAD (f _x)		SURVIVAL (l _x)		MORTALITY (d _x)		MORTALITY RATE (q _x)	
	M	F	M	F	M	F	M	F
0-1 ^b								
1-2	19	6	1.000	1.000	0.311	0.100	0.311	0.100
2-3	9	5	0.689	0.900	0.148	0.083	0.215	0.092
3-4	13	8	0.541	0.817	0.213	0.133	0.394	0.163
4-5	5	6	0.328	0.684	0.082	0.100	0.250	0.146
5-6	10	3	0.246	0.584	0.164	0.050	0.667	0.086
6-7	4	8	0.082	0.534	0.066	0.133	0.805	0.249
7-8	1	9	0.016	0.401	0.016	0.150	1.000	0.374
8-9	0	7	--	0.251	--	0.117	--	0.466
9+	0	8						
	<u>61</u>	<u>60</u>						

$$\bar{q}_{(M)} = 1/\sum l_x = 0.345$$

$$\bar{q}_{(F)} = 1/\sum l_x = 0.179$$

^aCalculations according to Table 8.4 in Caughley (1977:91).

^bSee Table 19 and text for independent estimates of mortality rates for this age class.

tertiary sex ratio favoring females. Klein and Olson (1960) believed that the unbalanced sex ratio favoring females in a lightly hunted population of blacktails in Alaska was due to higher natural mortality of males. Flook (1970), who specifically examined why adult females outnumbered adult males in populations of elk in Canada's western parks, concluded that non-harvest mortality of males older than yearlings contributed to the observed ratios.

Estimates of mortality rates for fawns (both sexes combined) were derived in a manner independent of life table analysis. The entire approach utilized data presented earlier for this population and was designed to provide robust estimates of q_x for each year from 1975-77. The estimates of mortality rate applied to fawns from June-November only, but since most fawn mortality occurred during this period, estimates of annual mortality rate would not be much higher. As an example, to calculate q_x for 1975, we started with the number of fawns per 100 does in November (from Table 9) and calculated ± 20 percent to bracket any error in our estimate of the actual fawn:doe ratio: 37 fawns ($\pm 20\%$)/100 does = 30-44 fawns/100 does. The lower estimate of 30 fawns/100 does and a population estimate of 180 in November 1975 resulted in an estimate of 34 fawns, 113 does and 33 bucks in the November population. Similarly, the estimate of 44 fawns/100 does resulted in a November population of 46 fawns, 104 does and 30 bucks. These 2 cases can now be used as preliminary information to derive minimum and maximum estimates of q_x , using 46 fawns:104 does and 34 fawns:113 does, respectively.

To continue the example, the minimum estimate of q_x was derived by taking the number of females in the November population (104) and adjusting this upward to account for female deaths since the previous June (fawn drop). The temporal distribution of female mortalities from 1974-76 indicated that 76% of all female deaths occurred from June-November. Since it was more difficult to locate carcasses during summer, it is more reasonable to assume that 80-90% of all female mortality occurred during that period. That is, 80-90% of 17.9% (\bar{q}_x) equals a 14-16% mortality rate for females during summer. To derive

our estimate of the number of June females in the minimum case (121), 104 was divided by 0.86 to replace the 14% lost during summer. Yearling females did not bear fawns; they were subtracted from the June population of females. To derive the number of yearling females in the June 1975 population, we used the number of fawns in November of the previous year (as above, with $\pm 20\%$ of fawn:doe ratios), assumed an equal sex ratio and divided these numbers in half (29-37). By subtracting 37 from 121, we arrived at a minimum estimate of the number of females giving birth in June (84). This number was multiplied by a fecundity rate of 1.7-1.9 to obtain the number of fawns born in June. Fecundity rates were based on limited reproductive information from this population, but seemed reasonable and in agreement with other studies of white-tailed deer (see Reproduction). The product of 84 and 1.7 yielded 143 fawns in June. Our example already contained an estimate of 46 fawns in November, thus, 97 fawns died from June-November, a mortality rate of 0.678. Note that in all calculations where a range in values existed, the value that would eventually result in a lower estimate of mortality rate was always chosen for the minimum case, and conversely, the value that would result in a higher estimate of q_x was always chosen for the maximum case. Both minimum and maximum estimates of q_x would tend to be conservative, since we assumed no mortality of fawns from November to the following June in arriving at the number of yearling females in the June population.

Estimates of fawn mortality rate (June-November) ranged from a low of 52-75% in 1977 to identical rates in 1975 and 1976 of 68-83% (Table 19). These rates, although indirectly calculated, were comparable to the rate of fawn mortality obtained for this same population in 1978, based on a study of radio-collared fawns. From June-November, 15 of 19 (79%) radio-collared fawns died of natural causes (A. C. Clark, pers. comm.).

Mortality rates of white-tailed deer fawns tend to be quite high in un hunted populations. Cook et al. (1971) found a mortality rate of 71% and 72% from birth to 3 months of age during a 2-year study of radio-marked fawns in Texas. White (1973:467) estimated a 60% mortality rate

Table 19. Derivation of estimates of mortality rate for white-tailed deer fawns during June-November on the CWT National Wildlife Refuge mainland.^a

	1975		1976		1977	
No. of fawns per 100 does in Nov. ($\pm 20\%$)	44	30	49	33	72	48
No. of fawns:does in Nov.	46:104	34:113	43:88	32:96	68:94	51:106
No. of females in Nov.	<u>Min</u> 104	<u>Max</u> 113	<u>Min</u> 88	<u>Max</u> 96	<u>Min</u> 94	<u>Max</u> 106
No. of females in June	121	135	102	114	109	126
No. of yearling females in June	37	29	22	15	25	17
No. of females giving birth	84	106	80	99	84	109
No. of fawns born	143	201	136	188	143	207
No. of fawns in Nov.	46	34	43	32	68	51
No. of fawns that died	97	167	93	156	75	156
Mortality rate (a_x)	0.678 68-83%	0.831	0.684 68-83%	0.830	0.524 52-75%	0.754

^aSee text for assumptions and discussion of an example calculation.

of fawns during summer on the Aransas National Wildlife Refuge in Texas. Hunted populations of whitetails generally have fawn mortality rates less than half as high as those from the unhunted populations cited above (O'Pezio 1978:2 Table 1).

Proximate causes of mortality. Systematic searches of the study area and incidental discoveries of carcasses led to the documentation of 155 deer mortalities from June 1974-December 1977 (Table 20). Each form of mortality listed can be considered a proximate cause. Mortalities were only assigned to nutritional stress if the fat content of the femur marrow was less than 20% or the marrow had such a high liquid content that analysis was impossible, and no other cause of death was determined. Since most carcasses were not obtained soon enough after death to perform a thorough necropsy and determine the exact cause, this list is, at best, only suggestive of the relative importance of each factor. The number of deaths attributed to automobiles, poaching and capture attempts was probably an accurate and nearly complete tally for the time period covered. The number of deaths due to other causes are conservative estimates of their importance.

Bone marrow fat content is one indicator of stored fat reserves and physical condition of an ungulate. Although several methods are available for quantification of percent fat in bone marrow (Verme and Holland 1973, Neiland 1970, Greer 1968), interpretation of these values is open to debate. Values greater than 80% are generally considered indicative of good condition and values less than 20% indicate an animal in poor condition. In Michigan, a value of more than 50% was taken to represent a white-tailed deer in minimal nutritional stress (L. J. Verme, pers. comm.).

The median fat content of the femur for a sample of 40 yearling and adult CWTM males was 54%; the median for 17 yearling and adult females was 62%. These samples included mortalities from all causes and seasons, but they indicated that the majority of deer examined were not in severe nutritional stress by Michigan standards, where weather is more extreme than southwestern Washington. Fifteen femur marrows were

Table 20. Proximate causes of mortality of white-tailed deer on the CWTN National Wildlife Refuge mainland during June 1974-December 1977.

<u>CAUSE OF DEATH</u>	<u>NUMBER DEAD</u>			<u>Number with symptoms of necrobacillosis</u>
	<u>Males</u>	<u>Females</u>	<u>Fawns</u>	
Accident ^a	1	0	1	0
Automobile	5	3	0	1
Capture kill	5	4	1	5
Coyote	0	0	9	0
Dog	5	0	0	4
Drowning ^b	0	2	1	2
Necrobacillosis (bacterial)	1	1	2	4
Nutritional stress	9	3	0	6
Poached	6	2	0	4
Unknown	<u>26</u>	<u>28</u>	<u>40</u>	<u>23</u>
Total (N=155)	58	43	54	49

^aIn both accidents, deer broke their necks after running into a fence; 1 of these had been frightened off a road by a passing automobile.

^bThere was some indication that 1 of the females that drowned had been chased into the water by dogs.

analyzed from CWTB that were poached, died during capture attempts or killed by automobiles ($\bar{x} = 71.7$, $SD = 30.4$) and compared to values from 42 CWTB that died from other causes ($\bar{x} = 50.5$, $SD = 28.7$). Mean fat content was significantly lower in this latter group, and these deer were presumably in poorer physical condition ($F_{1,55} = 5.85$, $P < 0.025$). This comparison emphasized the biased nature of inferring physical condition of the herd based on a sample of animals found dead of natural causes. The examination of 5 adult whitetails (3 males, 2 females) that were poached in a single incident on 23 February 1975, and assumed to be representative of the living, illustrated this particularly well. Each deer had abundant reserves of body and kidney fat, a femur marrow fat content of 99% and small numbers of internal parasites (only males examined for parasites). Both females were pregnant with twins.

Coyote predation. The criterion for attributing fawn mortalities to coyote predation was the presence of puncture wounds on the head or neck with evidence of hemorrhage about these bites (Cook et al. 1971). From June 1975-January 1976, 22 fawn carcasses were located and examined according to the above guidelines. Seven of 22 (32%) were definitely due to coyote predation, 2 were due to unknown causes other than predation and the remaining 13 deaths were due to unknown causes. This appraisal of coyote predation was almost certainly conservative, as 9 skulls from the latter 13 carcasses were never located and could not be checked for wounds. Twenty of 22 carcasses had been scavenged. There was no indication that coyotes killed any deer older than fawns, with 1 exception. In December 1974, an adult buck was attacked and severely wounded by 2 coyotes within 20 minutes of becoming partially immobilized by drugs; the male died several days later. Apparently, coyotes will engage large prey under certain circumstances, but the diagnostic pattern of wounds on the head or neck may be absent. Determination of the cause of death for a partially decomposed and scavenged carcass that had been killed by coyotes would be nearly impossible.

Dog kills. The interaction of factors that resulted in the death of a deer made interpretation of its causes complex. For example, an

adult male died after being chased into a drainage ditch by dogs in January 1976. Examination of the carcass the same day revealed heavy infestations of liver flukes (Fascioloides magna) and lungworms (Dictyocaulus viviparus) as well as a chronic injury to the right shoulder. The same deer had been observed for several days prior to its death with a severe limp, but fat content of the femur marrow was 79%, indicating this male was probably not under nutritional stress. We classified this mortality a dog kill, but had the carcass not been found so quickly, a different conclusion would have been reached. The remaining 4 deer known to be killed by dogs were also males in poor physical condition. Two of these had severe lungworm infections and the others had marrow fat content of 12% and 24%.

Necrobacillosis. An infection caused by a gram-negative, anaerobic bacterium, Fusobacterium (= Spherophorus) necrophorum, was isolated and found to be the cause of death in 4 deer (D. E. Olson, pers. comm.). This infection, most properly referred to as necrobacillosis (Rosen 1970:286), can manifest itself in a mammal in different ways, as suggested by several common names: necrotic stomatitis, ulcerative rumenitis, and foot rot. Although definitely diagnosed as the cause of death in only 4 whitetails, many deer were observed and carcasses were recovered with 1-4 feet grossly swollen and ulcerous, a condition referred to as foot rot. Since the pathogen was never actually isolated from any of these feet, we could not be positive that F. necrophorum was the infective agent. (This organism was isolated from other parts of the carcass in those deer positively diagnosed as having necrobacillosis). Rosen (1970:287), however, claimed there were no records of organisms other than F. necrophorum responsible for foot rot in deer, and "the pathology is typical enough to provide a presumptive diagnosis" (1970:289).

Males seemed to be afflicted more often by foot rot than females, but a direct comparison of its incidence between sexes was not possible due to seasonal differences in the acquisition of carcasses of each sex; this ailment was probably more common in winter when we obtained more male than female carcasses. We did document the number of deer observed

with a limp from February 1975-March 1976 by recording the sex of each limping deer only once per day, regardless of how often that deer was seen. Observations of that same deer the following day constituted an additional record. We then compared the observed number of limping male-days (41) and limping female-days (25) against the expected values based on the 1:3 male:female ratio in the population. The number of males that were observed limping relative to females during this 13-month period was significantly greater than expected ($G = 38.904$, $df = 1$, $P < 0.005$). As males were generally less observable than females in this population (see Table 5), the number of limping males observed was probably conservative.

Deer with a chronic case of necrobacillosis may develop alveolitis or osteomyelitis of the bony tissue surrounding the buccal cavity (T. P. Kistner, pers. comm.). A sample of 108 sets of skulls with mandibles from CWTD at least 1 year old was accumulated from the study area between 1972-77 and examined for possible symptoms of necrobacillosis. Twenty-one of 56 (37.5%) sets of skeletal material from males and 28 of 52 (53.8%) sets from females exhibited some indication of alveolitis or osteomyelitis. A higher percentage of female skulls and mandibles showed symptoms of this infection than did males ($G = 2.291$, $df = 1$, $P > 0.100$), but this may be expected due to the average older age at death for females and subsequent longer development time for a chronic infectious condition.

Fawns rarely displayed symptoms of necrobacillosis of the feet or bony tissue, but younger animals were not systemically checked for this, nor were fawn skulls routinely collected. As young animals generally develop an "acute, highly lethal form" of necrotic stomatitis (Wright 1958:520), one would not expect to observe symptoms in them characteristic of the chronic illness of older deer. Of 4 CWTD deaths directly attributed to necrobacillosis, 2 were 6-8-month-old female fawns. Neither of these had foot rot nor necrosis of the skull or mandibles.

Necrobacillosis can affect a deer in at least 3 ways:

1. The infection can metastasize to the liver, lungs, or brain, which results in death in a relatively short time

Rosen 1970:288).

2. Foot rot can impair mobility, predisposing that individual to predation.

3. Foot rot can disrupt a deer's normal activity patterns, having an adverse effect on nutrient intake.

Mech and Frenzel (1971:45) found that white-tailed deer killed by wolves (Canis lupus) in Minnesota had a significantly higher incidence of pathology of lower limbs than deer killed by hunters from the same population. While the last point (3) is difficult to substantiate, observations of grazing whitetails on the Refuge suggested this possibility. In January 1975, a yearling male was observed attempting to feed with a group of bucks with which he had been bedded. After repeated attempts to graze while standing, during which 1 front leg was periodically lifted off the ground, he knelt down on his front "knees" and grazed for a short time in this unusual position. He then resumed a bedded posture while the rest of his group continued to graze. One of the front feet of this male was swollen, presumably as a result of necrobacillosis. Also in January 1975, a female of unknown age was observed displaying the same behavior.

Many deer were affected by necrobacillosis, regardless of the assigned cause of death (Table 20). Of all mortalities located from June 1974-December 1977, 31.6% (49 of 155) exhibited some symptom of the infection. The percentage of deer at least 1 year old with such symptoms was 46.5 (47 of 101); 42.6% of the 54 deer that died of unknown causes, and were older than fawns, exhibited symptoms of this infection.

Using those natural mortalities for which we had analyzed samples of bone marrow, the mean fat content for those males with symptoms of necrobacillosis was 39.9 (SD = 25.3, N = 16), while the mean for those males without symptoms was 58.3 (SD = 32.2, N = 12). Although not a significant difference ($F_{1,26} = 2.88, P > 0.100$), this comparison suggested that the physical condition of males presumed to have necrobacillosis was inferior to those without symptoms of the infection at the time of death. There was no similar trend among females, but the sample available for this comparison was small (14).

Rosen et al. (1951) traced the history of epizootics of

necrobacillosis in California deer and thought that drought conditions that concentrated deer around muddy water holes typified those years when mortality was greatest. Concentration of animals on feedlots would have a similar effect, as Murie (1930) found for elk near Jackson Hole, Wyoming, where necrobacillosis was the major cause of winter mortality. The very wet and muddy conditions on the Refuge during winter, along with a high density of deer, probably created an ideal environment for the transmission of Fusobacterium. Males that entered winter in poor physical condition due to breeding activities in November would have lowered resistance to this infection; the pattern of male mortality following the rut could have been accentuated by the action of this pathogen.

Parasites. Eight whitetails were quantitatively examined for parasite "loads" prior to June 1974; 3 of these had parasite burdens of sufficient magnitude to cause debility or mortality (T. P. Kistner, pers. comm.). Each deer examined contained some internal parasites, with as many as 7 different species of helminths present in some individuals. cursory field examinations throughout the study revealed that most CWTD carcasses contained at least some helminth parasites. Gavin (in press) listed all species of parasites identified thus far from this population.

Ultimate causes of mortality. Based on the temporal distribution of natural mortalities of yearlings and adults in this population, the conclusion seems inescapable that mortality of these age classes resulted ultimately from the activities and stress associated with reproduction. For males, natural mortality was concentrated during that period after peak activity in rutting (November). At least 22 yearling and adult males died during November-January (1974-76), nearly twice as many deaths as any other 3-month period, and 70% of all male mortalities we located had died during November-April (Table 17). We did not believe that agonistic interactions between males directly influenced male mortality; all inter-male interactions observed by us were of such low intensity that physical injury to either buck was very unlikely.

Rather, we felt the major stress was due to increased energy utilization and movement by males in search of receptive females. French et al. (1955:34) observed that adult white-tailed deer males on complete and supplemented diets voluntarily decreased daily consumption of forage by half beginning with the November rut, continued to lose weight until late March and lost an average of from 20-42 pounds (9.1-19.1 kg) during this time, depending on the exact diet. Wood et al. (1962) showed a similar trend among several subspecies of O. hemionus. This cycle of weight loss during a critical environmental period (winter), the increased vulnerability to disease during sexual maturation in early fall (Magruder et al. 1957:7) and, presumably, the greater risk of physical injury due to increased activity of rutting males apparently resulted in substantial mortality of CWTM males.

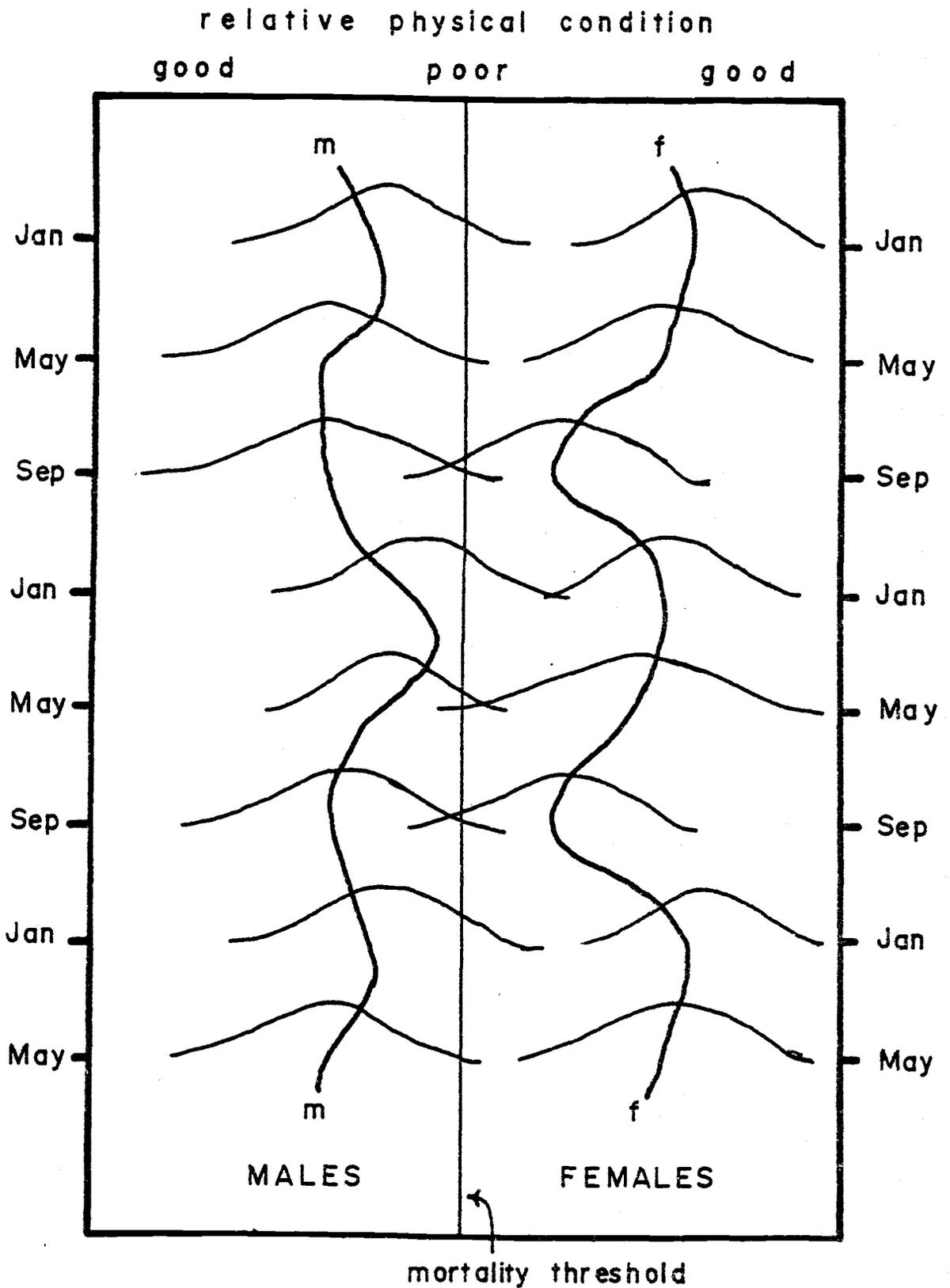
It appears that higher male mortality following the rut in ungulates with a polygynous mating system is common and may be generally explained by the above syndrome (Klein and Olson 1960, for black-tailed deer). Behavioral data for wild Soay sheep on the island of St. Kilda indicated that adult rams spent only one-fifth of the diurnal period grazing during the peak in mating activities, while ewes spent nearly 90% of daylight grazing (Grubb and Jewell 1974:168). A skewed sex ratio as high as 8 ewes per ram was attributed to higher male mortality (Grubb 1974a:256). McCullough (1969:90) found that Tule elk bulls decreased the percent of time spent bedded, the duration of bedded periods and percent of time spent feeding after acquiring a harem of cows; physical condition of harem bulls visibly declined through the time that they tended harems (1969:204-207). Similarly, Struhsaker (1967:111) observed that harem bulls of Rocky Mountain elk spent less time feeding than other sex-age classes. Flook (1970) demonstrated that during the rut, there was a heavy and rapid drain of fat reserves among adult bull elk, unlike females, accompanied by high physical activity and partial fasting. Heptner et al. (1961, in Geist 1971:302) believed that males of several species of sheep and antelope as well as the red deer (Cervus elaphus) suffered a higher mortality rate in winter that was proportional to their activity in the preceding rut.

Yearling and adult female mortality was heavier during August-October than during any other 3-month period (Table 17), and 71% of all female mortalities occurred during May-October. Since whitetail fawns are not fully weaned until at least 3 months old (Moen 1973:144) and energy requirements of the female are greatest at the peak of lactation (Moen 1973:362), CWTD females that were successful in raising fawns were probably under greatest nutritional stress in late summer-early autumn. Females whose fawns failed to survive after birth would have been under peak stress at late gestation in late May or June. Regardless of whether their fawns survived or not, adult females were most likely to succumb to physiological stress and/or any diseases associated with such stress during summer or early autumn.

Since median values of bone marrow fat collected from dead males and females on the Refuge were considerably higher than the level causing severe debilitation, some agent other than starvation must have caused the death of most of these deer. Numerous species of helminth parasites and a bacterial infection, whose symptoms were detected in 47% of all yearling and adult carcasses, could have accounted for this phenomenon.

There is a danger in using a statistical measure of "central tendency" such as a median to describe the physical condition of a cohort of deer: it de-emphasizes the actual distribution of individuals, which may spread from very good to very poor physical condition. We can plot the hypothetical mean of physical condition of a cohort of living males, for example, for several times during the year (Fig. 13). We then assume for purposes of illustration that the male cohort is normally distributed about this mean for each of these periods and that the mean fluctuates throughout the year in relation to the combined effects of extrinsic (environmental) and intrinsic stress on this cohort. Within the distribution about each mean, there are certain individuals whose combination of stress factors pushes that individual over the mortality threshold, a level of physical condition at which death is inevitable. Figure 13 depicts such a scheme for both males and females, incorporating our knowledge of CWTD mortality patterns and a blend of subjectivity. This approach only models mortality due

Figure 13. Mean physical condition of males (m) and females (f) through time in relation to the threshold of mortality. Also shown is the distribution of individuals' physical condition about this mean for selected months.



to increasing stress on the individual, as might occur against a background of reproductive activity, and does not include accidental deaths unrelated to stress that can occur to members of either sex at any time of year.

The model suggests several thought-provoking topics. Two of these, a cautionary note and an interesting question, are mentioned here. First, one must be careful in appraising the general health of this population based on an examination of dead animals found on the Refuge. A dead individual may have been in much worse physical condition than the "average" individual at that time of year, due to the set of circumstances peculiar to that animal before its death. As an extreme example, to infer the health of all deer based on an examination of adult males found dead during winter might be particularly misleading. Second, since male mortality was apparently linked to the "scramble" of individual males for receptive females, what was the reproductive success (e.g., number of copulations) during the rut of those males that crossed the mortality threshold the following winter relative to those males that survived?

Summary. The ratio of male to female mortalities (yearlings and adults) during winter was significantly greater than expected; the male:female ratio during summer did not differ significantly from expected. Fawn mortality was concentrated during summer; estimates of mortality rates for fawns ranged from a minimum of 52% to a maximum of 83% during June-November. During 1975-76, female mortality was heaviest in the central portion of the study area, while mortality of males and fawns was more uniformly distributed over the Refuge. Proximate causes of death included a bacterial infection, coyote predation, dogs, accidents and nutritional stress. Necrobacillosis may have been a major factor influencing mortality schedules and rates in this population. Rutting activities were apparently more stressful on the male segment of the population than fawning was for females. An annual mortality rate of yearling and adult males (0.345) that was twice as high as the rate for yearling and adult females (0.179) resulted in a skewed sex ratio that

favored females in the population and a greater median age at death for females. It could be quite misleading to infer the health of the population based on a sample of carcasses found on the Refuge.

Home Range and Movements

When full-time field studies resumed in June 1974, 14 collared deer remained in the population from the 1972-73 study. From June 1974-February 1976, an additional 42 CWTB were successfully collared and released. Of this total of 56 collared deer, only 3 were not accounted for as of March 1976, the last month of in-residence field research: 17 had died, 12 had lost their collars and 24 were still alive and collared. In total, 4275 observations of 44 collared whitetails were included in the following analyses.

Size of home range. Mean home range size for females was 112.9 ha using the convex polygon method and 158.5 ha with the determinant method; for males, mean area of home ranges with each method was 137.7 ha and 192.2 ha, respectively. Home ranges calculated in this way approximated the individual's lifetime range, since it included all "independent" location points collected on that deer (Table 21). For some deer, this included observations that spanned a 4-year period (e.g., Nos. 5, 17).

Home range areas calculated by the determinant method were usually larger (30 of 44) than when derived by the convex polygon method. However, Nos. 29, 54, 57 and probably B1 were known to grossly violate the assumption of a bivariate normal distribution with respect to intensity of use of the study area, by exhibiting a bimodal distribution of location points. This was most pronounced in deer Nos. 54 and 57, which established new, permanent home ranges in spring 1975 that were 2.5-3.0 km from their 1974-75 ranges. Estimates of home range size based on this distribution of location points were unreasonably high using the determinant method. Those deer, such as Nos. 28, 53 and 60, that had the majority of location points within a well-defined grouping, with a few points located far from this concentration (possibly as a result of 1 or 2 "exploratory" trips of short duration), exhibited

Table 21. Home range size of white-tailed deer on the CWT National Wildlife Refuge mainland calculated by both the convex polygon (C.P.) and determinant (DET) methods and the greatest straight-line distance between any 2 location points for each deer.

FEMALES (N=25)						
Deer #	Age at marking (months) ^a	Inclusive months of observations	No. months observed-No. observations ^b	SIZE (ha)		Greatest distance (m)
				C.P.	DET	
1	14	Aug 72-Sept 75	23-99	77.2	68.7	1349
5	≥27	Sept 73-Nov 77	23-87	95.2	113.7	1480
7	≥26	Aug 73-Nov 77	27-116	71.1	40.2	2271
10	≥32	Feb 73-June 76	32-142	129.9	141.1	2747
11	51	Sept 72-Aug 74	15-85	26.7	35.7	674
13	≥14	Aug 72-Nov 76	13-72	47.9	41.3	1188
17	8	Feb 73-Nov 77	38-311	80.0	79.9	1637
23	≥25	July 74-Nov 77	28-109	189.9	316.8	2303
25	11	May 75-May 77	16-45	73.6	96.8	2350
27	≥27	Sept 73-Nov 77	29-218	146.7	126.9	2632
28	8	Feb 75-Nov 77	21-162	148.9	92.9	3204
29	15	Sept 75-June 77	14-65	182.6	565.0	2996
31	≥32	Feb 73-Nov 77	38-339	69.5	68.2	1535
51	≥14	Aug 73-Nov 76	15-51	76.7	80.0	2080
52	13	July 74-May 77	22-97	61.5	72.8	1334
53	5	Nov 74-Nov 77	27-166	299.9	235.6	3631
54	14	Aug 74-June 76	23-192	312.6	519.3	3531
55	≥27	Sept 74-Aug 75	12-127	81.0	71.7	1319
57	7	Jan 75-Nov 77	21-100	159.0	553.1	3429
59	22	Apr 75-Nov 77	14-83	146.1	127.9	2189
70	44	Feb 75-July 75	6-65	39.6	54.2	941
71	7	Jan 75-Nov 77	22-173	61.0	63.0	1392
A3	≥29	Nov 75-May 77	8-35	89.9	127.1	2625

Table 21. continued.

Deer #	Age at marking (months) ^a	Inclusive months of observations	No. months observed-No. observations ^b	SIZE (ha)		Greatest distance (m)
				C.P.	DET	
A4	65	Nov 75-May 77	12-64	108.9	190.8	2819
A7	19	Jan 76-Nov 77	10-39	45.9	79.8	1255
			MEAN 20.4-121.7	112.9	158.5	2116
			SD 8.7-78.3	73.4	159.3	864
MALES (N=19)						
3	6	Dec 75-May 77	10-23	83.4	167.3	2229
15	18	Dec 72-Jan 75	14-88	185.4	291.0	2916
21	0.5	June 75-Nov 76	11-48	43.6	56.4	1269
22	14	Aug 73-June 76	13-47	175.2	227.5	3034
38	38	Aug 73-July 75	14-88	253.0	302.4	2785
40	≥33	Mar 73-Aug 73	5-30	84.9	209.8	1395
60	≥27	Sept 74-Jan 77	22-131	305.3	246.8	3217
67	7	Jan 75-Nov 75	11-83	38.9	41.7	1258
69	55	Jan 75-Feb 76	13-101	76.5	92.4	1540
82	6	Dec 74-June 76	19-127	121.2	112.6	2400
83	18	Dec 74-Mar 75	4-33	44.7	93.7	1074
84	6	Dec 74-Nov 75	11-104	149.3	130.0	2321
85	20	Feb 76-Nov 77	5-23	171.3	331.3	2824
86	8	Feb 75-Feb 76	13-89	242.5	208.9	2923
88	≥29	Nov 75-Nov 77	8-44	134.9	214.4	1795
116	0.5	June 75-Nov 76	13-51	102.7	179.8	2305
118	0.5	June 75-May 76	12-71	34.6	41.1	1389

Table 21. continued.

Deer #	Age at marking (months) ^a	Inclusive months of observations	No. months observed-No. observations ^b	SIZE (ha)		Greatest distance (m)
				C.P.	DET	
B1	19	Jan 76-Nov 77	7-20	191.6	452.7	4572
62	17	Nov 74-Apr 75	6-32	177.5	251.6	1967
			MEAN 11.1-64.9	137.7	192.2	2274
			SD 4.7-35.9	78.4	108.7	884

^aJune was assumed to be the month of birth of all deer. Age at marking for some individuals determined by aging skull after death.

^bNumber of months in which this deer was actually observed-total number of observations for all months.

larger estimates of home range size with the convex polygon than with the determinant method.

More meaningful comparisons of home range size were possible by partitioning marked deer into 6 sex-age classes, rather than comparing all males to all females. We utilized only estimates of home range derived from the determinant method to compare these classes, due to its statistical stability and lack of sample size bias (Jennrich and Turner 1969:235-236). By computing separate estimates of home range for each age class (i.e., using points collected from 1 June-31 May to calculate home range size for fawns and yearlings, rather than combining all points over an individual deer's life), the problem of a bimodal distribution of location points was greatly reduced for all individuals except No. 57. We, therefore, used only location points obtained before her shift in April 1975 to estimate her home range as a fawn, instead of following our usual procedure of using all locations collected until 1 June. An estimate for No. 57 as a yearling was not used in the analysis because of a bimodal distribution within that year.

Mean area of home range was smallest for male fawns (65.4 ha) and largest for adult males (208.6 ha) (Table 22). There was a trend for home ranges to become smaller with increasing age among females and larger with increasing age among males. An adult female, No. 23, had the largest home range (316.8 ha); No. 82, a male fawn, had the smallest (18.6 ha). A 1-way analysis of variance among all 6 means resulted in a significant F value ($F_{5,46} = 3.78, P < 0.01$). A mean separation test (Student-Newman-Keuls) indicated that 3 pairs of means were significantly different ($P < 0.05$): male fawn-male yearling, male fawn-male adult, and female adult-male adult (Table 22).

Since the density of this population decreased from 1974-75 to 1975-76 as already discussed, one might expect a change in the size of an individual deer's home range through this period, as alluded to by some authors (Sanderson 1966:219). Only 7 adult females and 1 adult male that were collared were observed often enough to calculate home range for both years. Since we completed full-time field work in March 1976, we utilized data only from June 1974-March 1975 and

Table 22. Comparison of estimates (determinant method) of home range size among sex-age classes of white-tailed deer on the CWT National Wildlife Refuge mainland. (Range of values in parentheses).

Age	N	Mean number of months observed ^a	FEMALES		
			Mean number of observations	Home range (ha) Mean ^b	SD
Fawn	5	5 (4-7)	48 (26-70)	154.5 (49.4-293.6)	92.9
Yearling	9	10 (5-12)	67 (27-124)	113.6 (37.2-274.3)	73.7
Adult	18	19 (6-38)	112 (35-339)	103.6 (35.7-316.8)	69.8
MALES					
Fawn	7	7 (4-12)	57 (41-88)	65.4 (18.6-184.7)	56.1
Yearling	6	7 (4-12)	44 (21-77)	187.2 (54.1-316.2)	111.4
Adult	7	11 (5-22)	68 (30-131)	208.6 (92.4-302.4)	65.2

^aFawns and yearlings can be observed for a maximum of 12 months only before advancing to the next age class.

^bPairs of means from the following sex-age classes were significantly different using Student-Newman-Keuls' test ($P < 0.05$): adult female-adult male, fawn male-yearling male, and fawn male-adult male.

June 1975-March 1976 for each deer to increase comparability between years. Mean size of home range for adult females in 1974-75 ($\bar{x} = 108.1$ ha, SD = 91.9) was not significantly different from the mean ($\bar{x} = 87.8$ ha, SD = 51.5) in 1975-76 ($F_{1,12} = 0.25, P > 0.50$). Five females decreased home range size while 2 showed increased size from the year of higher density to the year of lower density. There was no consistent pattern between home range size and fawning success for this sample of 7 females. Adult male No. 60 exhibited a decrease in home range size over the same period from 213.3 ha to 90.4 ha.

Movements of 1 female group were intensively observed from a tower and blinds for an entire day to acquire an understanding of daily use of home range. Two adult females, Nos. 31 and 17, and the latter's male fawn (No. 86) were observed continuously from 0920 28 March 1975 to 0530 29 March 1975. Thick fog prevented further observations on 29 March. Using the convex polygon method, this trio, which remained together the entire time, ranged within an area containing only 5.9 ha. During the day the group remained under or adjacent to a small grove of trees that was located next to a tall-grass field. At dusk, they moved to a short-grass pasture to feed, where they stayed, alternately grazing and bedding about 80 m from the perimeter road, until 0530 29 March. It was our impression that this pattern of limited use of the total home range on a daily basis typified the movements of many deer, especially females. This pattern of use would then shift from week to week so that home range size that was based on several months' data was much larger than the daily area. For example, Nos. 31 and 17 had respective home ranges of 69.5 ha and 80.0 ha, using the convex polygon method and all data points obtained for these deer. This was approximately 12 times larger than the daily range for 28-29 March 1975.

A male yearling, No. 68, moved 4970 m between the date he was marked on 11 November 1974 and the date of last observation, 9 December 1974. This was the greatest straight-line distance recorded between any 2 location points for a marked individual. No. 68 was not included in Table 21, since he was observed a total of only 9 times before his death in December 1974. The greatest distance between the extreme ends of the

study area is approximately 5640 m. On the average, however, males and females had maximum distances between their most extreme location points that were less than half the length of the study area. This suggested that CWTB on the Refuge were not familiar with the entire study area, although movements of short duration during the life of an individual could have been undetected by us. The mean distance in meters between extreme location points for males ($\bar{x} = 2274$, $SD = 884$, $N = 19$) was only slightly longer than the mean for females ($\bar{x} = 2116$, $SD = 864$, $N = 25$). It should be noted that females were observed about twice as often and in twice as many months as males (Table 21).

Severinghaus and Cheatum (1956) summarized the literature published prior to 1956 regarding size of white-tailed deer home ranges and the existence of seasonal movements and migrations in geographical areas that have severe winters. Their generalization that the seasonal range of an individual deer rarely exceeds 1.6 km in diameter has generally been supported by studies conducted since that time. Thomas et al. (1964), Alexander (1968) and Michael (1965) found that whitetails in Texas have home ranges with a radius less than 2.4 km and that males usually have larger ranges than females. Mean maximum distance moved by females was 2.3 km and for males 3.1 km in Missouri (Progulske and Baskett 1958), slightly smaller ranges were found in Indiana whitetails (Kirkpatrick et al. 1976) and home ranges in the Southeast were stable and only 50-150 ha in size (Byford 1969, Kammermeyer and Marchinton 1976, Marshall and Whittington 1968). Home ranges of whitetails in Texas and the Southeast seemed most similar to those of CWTB on the Refuge with respect to size and temporal stability.

Shape of home range. The shapes of home ranges were strongly influenced by the presence of road and water boundaries on the Refuge. On only 1 occasion did whitetails flee from us by swimming a slough, even though deer fled from our approach on foot literally thousands of times. This avoidance of water resulted in home ranges that were restricted to 1 side of sloughs and ditches that were too wide to jump across, a situation found also by Michael (1965:50) in Texas.

Dispersal and home range stability. Howard (1960) defined dispersal as movement of an animal from its birthplace to breeding place, and dispersal distance as the straight-line distance between these locations. With this in mind, then, any deer that survived until its 1st reproduction would have a dispersal distance, regardless of how small that might be. It would be untenable, given this definition, to refer to such an individual as a non-disperser, even if it bred only 200 m from the site where it was born. We preferred to adopt the terminology short-disperser and long-disperser, rather than to discuss conspicuously long movements of individual deer as dispersal and ignore the rest. This was a broader approach to the concept of dispersal than generally found in the literature on deer movements, where dispersal was neither rigorously defined nor discussed with regard to its importance for the population.

Distance between annual centers of activity of an individual deer was used as a crude indication of spatio-temporal stability of home range and dispersal. These geometric centers of activity were identified by taking the mean of all x-coordinates and the mean of all y-coordinates for a given period of time. A change in the intensity of habitat utilization by a deer or an actual shift in home range would be reflected in a change in center of activity.

We calculated distances between annual centers of activity for 8 different deer observed as fawns and yearlings and for 5 deer observed as yearlings and 2-year-olds (Table 23). If we assume that fawns were captured and marked in the natal area, which is reasonable given the sedentary nature of adult females, these calculations indicated that dispersal distance for all but 2 deer was extremely small. Nos. 54 (yearling female) and 57 (fawn female) established a permanent home range together approximately 2000 m away from No. 57's natal area, which was also the area inhabited by No. 54 prior to this shift in April 1975. We did not know the location of No. 54's natal area. Although from an area of higher to lower density on the Refuge, these shifts in home range did not expand the range of the population or reduce the overall density of the Refuge population.

Table 23. Straight-line distance between annual geometric centers of activity for marked white-tailed deer observed as fawns and yearlings and for marked individuals observed as yearlings and 2-year-olds.

Deer #	Sex	NO. OF OBSERVATIONS ^a		Fawn-yearling distance (m)
		As fawn	As yearling	
17	F	37	26 ^b	297
28	F	47	103	159
53	F	60	89	42
57	F	26	58	1702
71	F	70	92	159
67	M	62	21	213
82	M	49	77	230
86	M	43	46	264

Deer #	Sex	NO. OF OBSERVATIONS ^a		Yearling-2-year-old distance (m)
		As yearling	As 2-year-old	
1	F	27	72	215
17	F	26 ^b	119	66
52	F	55	42	213
54	F	124	68	2135
15	M	54	34	187

^aUnless otherwise noted, centers of activity were derived for those deer observed in at least 4 months and a minimum of 20 times, using observations from June through the following May.

^bIncluded observations only from June-August.

Distances between annual centers of activity were also calculated for 10 marked adults (Table 24). None of these deer (8 females, 2 males) shifted more than 330 m between one year and the next, an insignificant distance due to the potential for long distance movement by this mammal. Furthermore, no individual was known to disperse from the Refuge: 53 of 56 collared deer in the population could be accounted for by the end of full-time field work in March 1976. It was possible that 3 adult females that disappeared during the study had moved off the Refuge, but circumstantial evidence indicated that mortality was a more likely explanation in each case.

Two females, Nos. 17 and 31, exhibited a remarkable sedentary tendency throughout a 5-year period. Center of activity for No. 17, who was born to No. 31 in 1972 and maintained a strong social bond with her during these 5 years, moved 297, 66, 89 and 66 m between the years she was a fawn and 5 years old, respectively. That these shifts were not a steady progression away from the natal area was indicated by the distance between her centers of activity as a fawn and as a 5-year-old, 225 m. No. 31's center of activity moved 330, 89, 118 and 89 m between the years 1972-73 and 1976-77, the same years for which data on No. 17 were collected. The distance between No. 31's 1972-73 center of activity and that of 1976-77 was 278 m.

A pattern of dispersal that differed somewhat for males and females became apparent after calculating annual centers of activity using all observations for each deer, regardless of the minimum number. For 6 females that were marked as fawns and observed until 3 years old, only the geometric center of activity of No. 57 shifted a significant distance from her natal area (Fig. 14). Of 7 males marked as fawns and observed when older, only No. 82 was observed as an adult, and in fact, died during the month of his 2nd birthday. However, Nos. 83, 3 and 84 had already displayed significant shifts in their centers of activity based on limited observations (Fig. 15).

A tendency toward greater dispersal by males was supported by data on the distance between the location where a whitetail was marked and the point where it was found dead. This method was independent of

Table 24. Straight-line distance between annual geometric centers of activity for marked white-tailed deer adults on the CWT National Wildlife Refuge mainland.

<u>Deer #</u>	<u>Sex</u>	NUMBER OF OBSERVATIONS ^a					<u>Distance (m)</u>
		<u>72-73</u>	<u>73-74</u>	<u>74-75</u>	<u>75-76</u>	<u>76-77</u>	
5	F	--	--	53	28	--	238
7	F	--	--	52	51	--	30
10	F	--	25 ^b	52	63	--	189,238
17	F	--	--	119	107	22 ^c	89,66
23	F	--	--	40	59	--	250
27	F	--	--	110	87	18 ^c	66,177
31	F	35	24 ^d	124	130	19 ^c	330,89,118,89
51	F	--	--	21	27	--	125
60	M	--	--	77	51	--	301
69	M	--	--	67	34	--	225

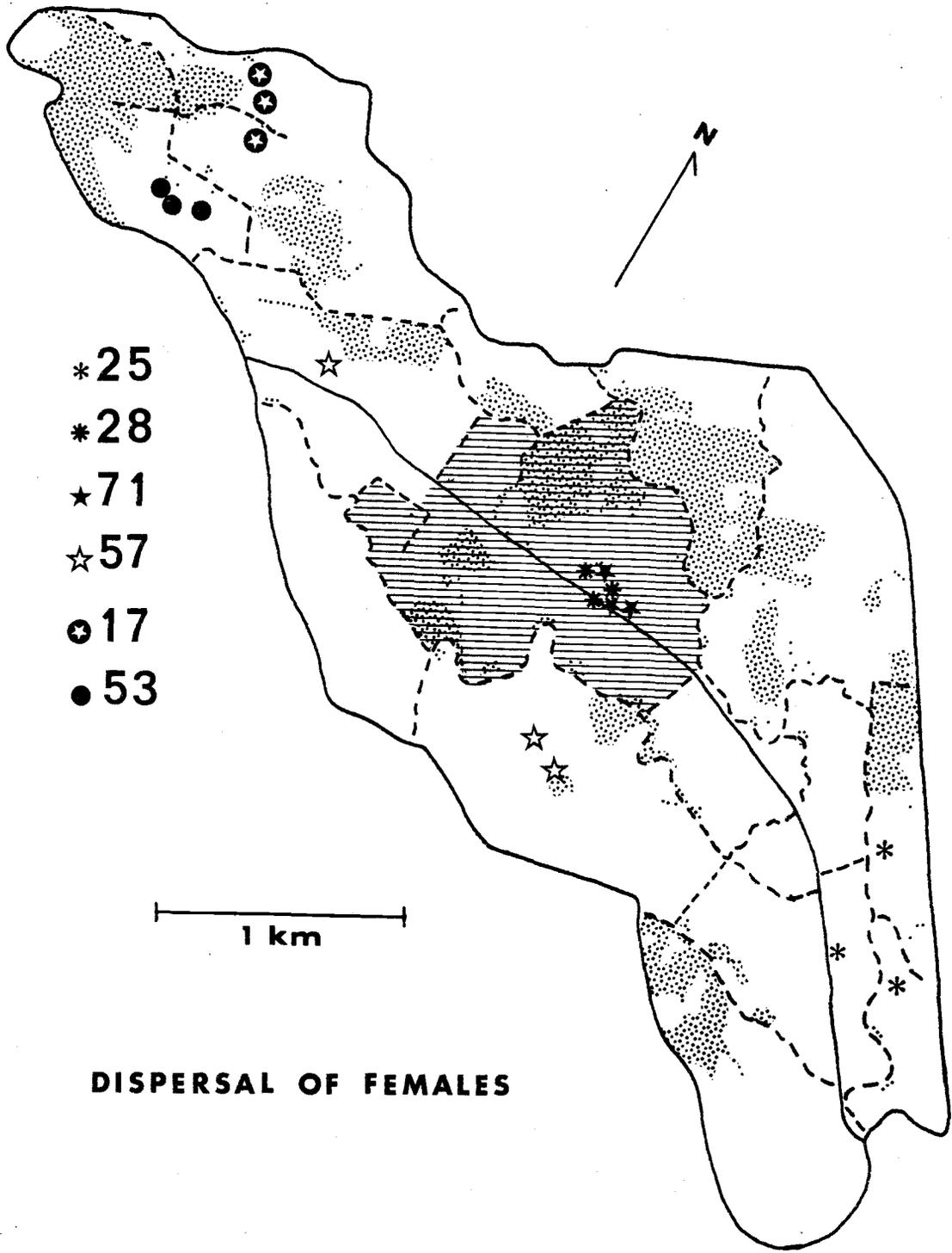
^aUnless otherwise noted, centers of activity were derived for those deer observed in at least 4 months and a minimum of 20 times, using observations from June through the following May.

^bIncluded observations only from February-September 1973.

^cIncluded observations through November 1977.

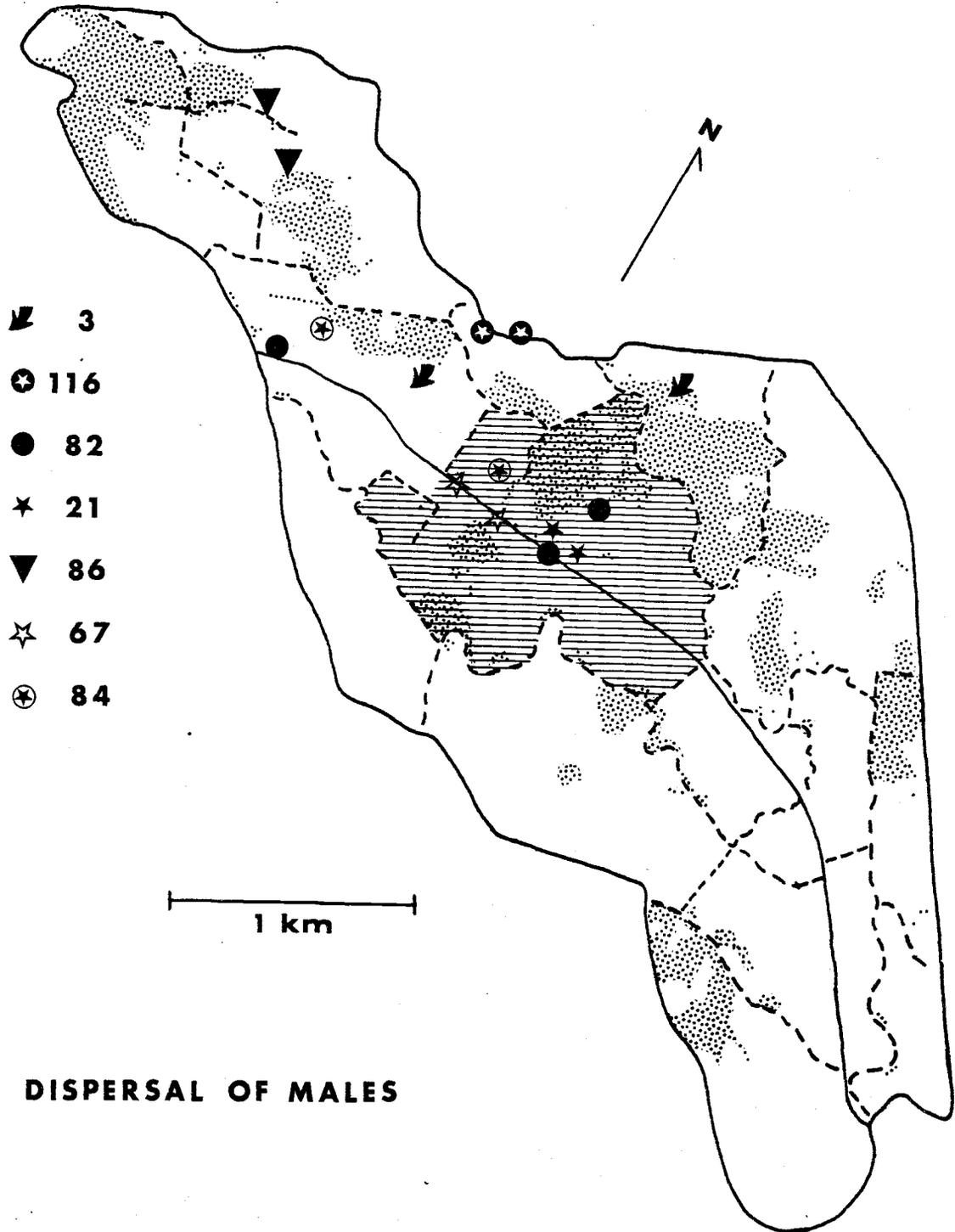
^dIncluded observations only from June-August 1973.

Figure 14. Annual centers of activity for 6 collared white-tailed deer females that were observed as fawns, yearlings and 2-year-olds on the CWTD National Wildlife Refuge mainland.



DISPERSAL OF FEMALES

Figure 15. Annual centers of activity for 7 white-tailed deer males that were marked as fawns on the CWTN National Wildlife Refuge mainland.



the center of activity approach. Only deer that were known to be alive at least 3 weeks after marking were included in this analysis. Nine females that had lived an average of 13.4 (1-35) months after capture had a mean distance of 397 (42-1085) m between their capture and death locations. Although 10 males that had lived an average of 13.6 (1-28) months after capture were found dead a mean distance of 1060 (172-3489) m from their capture locations, this was not significantly different than the distance for females ($F_{1,17} = 3.55, P > 0.05$).

Although there are no absolutes regarding which members of a deer population will exhibit long-distance dispersal or why, dispersal appears to be more common among yearlings than other age classes and more common among males than females. In Illinois, Hawkins et al. (1971) found annual dispersal rates of white-tailed deer from a refuge of less than 4%, 13% and 7% for fawns, yearling does and adult does, respectively, and rates of slightly more than 80% and 10% for yearling and adult males, respectively. Hawkins et al. (1971) were certain that lack of food or condition of the habitat were not the cause of this dispersal. In an analysis of 2 sex-age classes of tagged whitetails in Indiana, 62% of 29 yearling males were recovered more than 1.8 km from location of marking as compared with only 30% of 54 adult females (Kirkpatrick et al. 1976). For mule deer in Utah, 62% of 92 males and 40% of 45 females that were marked as fawns were killed as older deer more than 1.6 km from location of marking (Robinette 1966:342). In these examples of long-distance movement by deer, actual dispersal distance can not be substantiated (given our definition) without knowing exactly where an individual was born and where it bred. As this is usually not possible, these studies only suggest that some (perhaps many) members of a population breed away from their natal area. In contrast, long-distance dispersal in black-tailed deer in California chaparral was not detected. Those young deer that could be recognized remained near their place of birth; Dasmann and Taber (1956:156) concluded that the usual method this population spread into new habitat was by "slow diffusion."

An individual's movements can have at least 3 "unselected" consequences for the population to which that individual belongs:

distributional, density-related and genetic. First, the existence of long-dispersers would provide the potential for range expansion of the population into habitat not occupied or only sparsely occupied by that taxon. Second, long-distance dispersal of individuals could result in lower population density than would otherwise be attained, as Strandgaard (1972) found for a roe deer (Capreolus capreolus) population in Denmark. Data on CWTM movements (i.e., lack of movement off the Refuge) did not substantiate either of these effects as being important to the Refuge population. Third, the genetic influence of dispersal on a population, although difficult to measure directly, should be an important reason for understanding this type of movement. Sanderson (1966:231) argued that the reasons for animal movements are more important than the movements [distances] themselves. However, the distance between an animal's natal area and the location where it breeds can be of genetic importance. Wilson (1975:103) implied that short-dispersers were more likely to breed with genetically related conspecifics than were long-dispersers, which would result in "small effective population size, greater inbreeding, and a steady loss of genetic variability" to small, semi-isolated groups. Mayr (1963) believed there was a genetic basis for individuals to be short-distance or long-distance dispersers. The potential genetic effects of dispersal on the CWTM population need further examination; dispersal distance is germane to the calculation and discussion of effective population size of the Refuge herd, which is treated in a later section.

Exclusivity of home ranges and territoriality. Home ranges of marked deer that belonged to the same social group were essentially identical, but the ranges of all marked deer overlapped greatly with those of marked and unmarked deer of all sex and age classes. However, for several females (Nos. 27, 17, 31), we were able to identify certain small areas within their respective home ranges that were regularly used by them as bed sites. These sites were easily observed from the perimeter road of the Refuge and were rarely occupied by deer other than the marked female that inhabited that area. Well-drained,

relatively dry sites used for bedding appeared to be limited in number during winter when standing water on the Refuge made low-lying areas undesirable. CWTB were never observed to lie down where there was surface water and, in fact, avoided moving through such areas. On several occasions, a marked female was observed to interact with a "transient" female in the vicinity of one of these bed sites, often getting up from her bedded position to initiate the interaction. In every case, the marked female displayed dominance by slowly walking straight toward the other female with her ears laid back alongside her head, a threat posture termed "ear-drop" by Thomas et al. (1965:319). The "transient" female would lower her head, turn and leave the area at a slow run. Usually the marked female would pursue the "transient" no further, but sometimes she would chase the submissive female 20-40 m. Defense of a fawn was not the explanation for these interactions, as the marked female often did not have a fawn at heel.

Although dozens of agonistic interactions (of low intensity) among males were observed by us, the result differed from the few interactions we observed among females. The subordinate male did not leave the area where the interaction occurred, but resumed grazing a few meters from the dominant male or interacted with another male nearby. Also, the dominant male lost interest in the presence of the submissive male soon after the interaction.

If we adopt Brown's (1975:61) definition of territory as "a fixed area from which intruders are excluded by some combination of advertisement (e.g., scent, song), threat, and attack," then CWTB females may have been territorial with respect to certain sites within their home ranges. The term "territoriality" has been almost universally avoided in the literature on North American cervids, possibly, because individuals of the populations studied were not territorial, displayed a subtle form of territoriality that would only be detected after months of intensive observations of marked individuals, or because emphasis was placed on examining the wrong sex (male) for this form of spacing behavior. Miller (1974) was an exception, and applied the term to 4 types of behavior he observed in black-tailed deer in western Oregon.

One type, defense of fawn, would not be valid using Brown's definition above. However, Miller documented active defense of an area against other males by 1 adult buck during the rut, repeated expulsion of intruding deer by individual members or the entire group of resident deer (mostly females and fawns) within a defended portion of the latter's home range, and on 16 occasions throughout 1 year, defense of a 9.5 ha area by 1 adult doe with a total home range of 57.5 ha.

Care must be taken when attempting to interpret displays of social behavior, especially when they were not rigorously quantified. Our tentative conclusion was, however, that interactions among CWTD males, which usually occurred between males that had been bedded or feeding together, did not greatly influence dispersion of males or females on the Refuge. Agonistic interactions among females may have acted as a spacing mechanism for this sex. Similar conclusions were reached by Dasmann and Taber (1956:160) for a population of black-tailed deer; centers of activity for males showed a tendency toward aggregation, while mutual antagonism among females resulted in "spacing ecologically similar to what would be found if the home range centers were actually defended territories."

Summary. Estimates of home range size for females averaged 112.9 ha using the convex polygon method and 158.5 ha using the determinant method and 137.7 ha and 192.2 ha for males, respectively. Mean home range size was smallest for male fawns (65.4 ha) and largest for adult males (208.6 ha) among 6 sex-age classes examined. Mean home range size for 8 adults during a year of higher population density did not increase when compared to a year of lower density. Shapes of individual deer's home ranges were strongly influenced by road and water boundaries. Distance between annual centers of activity indicated that home ranges had high temporal stability; no marked deer was known to disperse from the Refuge. There was a tendency for males to disperse longer distances than females on the Refuge. Observations of agonistic interactions suggested they may have acted as a spacing mechanism for adult females, but not for males.

Genetic Considerations

A major consideration when dealing with insular or near-insular populations of animals is the amount of genetic variation present in the population. This is particularly important for endangered species, which generally consist of a small number of individuals divided into insular populations. Genetic variation is responsible for setting the magnitude of any evolutionary changes that occur in the population, according to the Fundamental Theorem of Natural Selection: the rate of evolution is proportional to the genetic variance of the population (Wilson and Bossert 1971:79). Theoretically, the less genetic variance present in a population and therefore the less potential for evolutionary change, the less that population should be able to cope with changes in its environment relative to other populations of the same taxon having a greater amount of genetic variance.

Without the counteracting effects of selection and mutation, genetic variation (heterozygosity) is lost each generation, with the rate of loss dependent upon population size. The relationship between the fraction of non-identical genes that become newly "inbred" each generation (ΔF) and size of the population is:

$$\Delta F = 1/2N \quad (\text{Spiess 1977:320}). \quad \text{Equation 12}$$

However, N refers to the size of an "idealized" population; that is, one where opposite sex gametes have equal chances of fusing with each other irrespective of the donors' genetic relationship (= random mating). Furthermore, N is based on the assumption of an equal number of parents of each sex, each of which contributes an equal number of gametes to the next generation. It is certain that this latter assumption did not hold for the population of CWTB on the Refuge mainland.

Effective population size. To calculate the loss of heterozygosity per generation from Equation 12, "effective" population size (N_e) must be derived and substituted for N . This exercise is desirable not only to appraise the potential loss of heterozygosity, but "it is important biologically to determine just how different the effective number of

parents may be from the apparent size of the population" (Spiess 1977: 326).

If we let k_i be the number of successful gametes from the i^{th} parent in the $t-1$ generation; then,

$$\bar{k} = \frac{N_0}{\sum_i k_i} = \text{average number of successful gametes from any parent, where } N_0 = \text{number of parent individuals.} \quad \text{Equation 13}$$

Then, $N_0 \bar{k} = 2N_1$ = number of successful gametes (i.e., those producing N_1 progeny). Effective population size can then be expressed for a population of dioecious organisms:

$$N_e = \frac{2N_1 - 2}{(\sigma_k^2 / \bar{k}) + \bar{k} - 1}, \quad \text{Equation 14}$$

where variance in k (σ_k^2) relates the distribution of k successful gametes among the parents:

$$\sigma_k^2 = (k - \bar{k})^2 / N_0. \quad \text{Equation 15}$$

The complete derivation of these formulae are found in Spiess (1977: 325-326).

To illustrate the relationships of sex ratio, mating system and total population size with N_e , 8 derivations of N_e that ranged from 47-326 were calculated (Table 25). Population estimate and herd composition data for November 1976 were used to calculate N_e in this exercise. For example, if the population had contained only breeding adults in a 1:1 sex ratio under a strict monogamous mating system, $N_e = 326$; this number is nearly twice as high as the actual population size (164). N_e decreased to 250 when there were 126 adults under the same conditions and then dropped sharply to 139 when the actual number of males (35) and females (92) were used. This latter estimate still assumed equal breeding among the individuals within a sex. N_e fell even lower (99) after subtracting yearling males, which probably do not breed in this population, from the male cohort. Finally, after incorporating

Table 25. Models of effective population size (N_e) for white-tailed deer on the CWT National Wildlife Refuge mainland in November 1976, under various schemes of sex ratio and male mating success.^a

Total no. of female parents (Female parents x no. of successful gametes per female)	Total no. of progeny (N_1)	Total no. of male parents (Male parents x no. of successful gametes per male)	Total no. of parents (N_0)	Total no. of successful gametes ($2N_1$)	Mean no. of successful gametes per parent (\bar{k}) ^b	σ_k^2 ^c	N_e ^d
82 (82 x 2)	164	82 (82 x 2)	164	328	2.00	0.00	326
63 (63 x 2)	126	63 (63 x 2)	126	252	2.00	0.00	250
92 (92 x 2)	184	35 (35 x 5.26)	127	368	2.90	2.12	139
92 (92 x 2)	184	25 (25 x 7.36)	117	368	3.15	4.83	99
92 (77 x 2, 15 x 1)	169	25 (25 x 7.36)	117	338	2.89	4.18	101
92 (77 x 2, 15 x 1)	169	25 (1 x 30, 20 x 6, 3 x 5, 1 x 4)	117	338	2.89	9.04	67
92 (77 x 2, 15 x 1)	169	25 (2 x 20, 2 x 18, 6 x 10, 1 x 5, 14 x 2)	117	338	2.89	12.61	54
92 (77 x 2, 15 x 1)	169	25 (9 x 16, 1 x 10, 15 x 1)	117	338	2.89	15.09	47

^aFrom Table 10, population contained 35 males, 92 females and 38 fawns ($N=164$).

$$b \bar{k} = 2N_1/N_0$$

^c $\sigma_k^2 = \sum(k-\bar{k})^2/N_0$, where k is the number of successful gametes from each parent.

$$d N_e = 2N_1 - 2/(\sigma_k^2/\bar{k}) + \bar{k} - 1$$

differential male and female reproductive success into the model (which increased σ_k^2), N_e dropped substantially. Although we did not know with certainty the relative mating success among males or among females, we employed 3 polygynous breeding schemes for males with 1 fecundity schedule for females to derive our estimates. Based on our earlier appraisal of female fecundity (1.7-1.9), we utilized 77 females bearing twins and 15 females bearing single fawns. Fifteen is also a reasonable estimate of the number of yearling females in the population in November 1976, the age class most likely to bear fewer fawns. Calculation of effective population size for the Refuge mainland population of CWTD ranged from 47-67, depending on which polygynous breeding scheme for males was used. It is generally accepted that white-tailed deer have a polygynous mating system and males exhibit a dominance hierarchy that influences male reproductive success (Hirth 1977, Brown 1974, Gavin, pers. obs.). This variance in productivity among individuals lowered the effective population size to 29-41% of total population size, which was considerably lower than the N_e/N ratio of 63-94% for drosophila, a snail (Lymnaea) and humans (Crow and Morton 1955, Crow 1954, in Spiess 1977:330).

Although the actual sex ratio in the population and differential success of individuals could be included in our model, the underlying assumption that each individual mated randomly was not testable. Inferences could be made regarding this assumption if we knew whether males exhibited a significant preference or avoidance of their natal area for breeding. The area in which CWTD males were born would presumably contain females of closer genetic relationship to them than would other areas on the Refuge (see Dispersal and home range stability). Preference for breeding in the natal area would decrease N_e even further, while significant avoidance of this area would tend to increase it. Male whitetails were found to leave a non-hunted refuge and move into adjacent hunted lands during the rut in Georgia (Kammermeyer and Marchinton 1976). Assuming these males were born on the refuge, they actually increased their dispersal distance by moving away (temporarily?) from their natal area to breed, according to the

definition of dispersal distance by Howard (1960). More accurate estimates of N_e for the Refuge population of CWTB must await collection of detailed behavioral data during the breeding season.

Rate of fixation. Returning to Equation 12, there would be a rate of inbreeding increment each generation of 0.007-0.011, depending on which derivation of N_e was used in the formula (i.e., 67, 54, 47). It is not difficult to envision the combined effects of mutation and selection overriding this 1% fixation rate. Additionally, gene flow from adjacent populations that exceeded this value (i.e., $>1/2N_e$) would "effectively order the gene frequency distribution among populations of neutral genotypes; if the opposite is true, fixation would predominate due to random genetic drift" (Spiess 1977:653-654). To prevent fixation of homozygotes in the Refuge mainland population of CWTB, only about 1 migrant per generation (0.82-1.29) would need to successfully breed in the population. Although we detected no movement of whitetails onto the Refuge study area, such a small immigration rate would be difficult to document; such movement of whitetails from islands in the Columbia River to the study area would be highly probable.

Summary. A model for calculating effective population size (N_e) resulted in values that ranged from 29-41% of total population size for the Refuge mainland. High variance in productivity among individuals was responsible for an N_e/N ratio that was considerably lower than those calculated for several other organisms. We were not able to test the assumption of random mating inherent in the determination of N_e , but it is probable that if males exhibited a significant preference or avoidance of their natal area for breeding, N_e would have been lower or higher, respectively. Rate of fixation of homozygotes was then estimated at approximately 1% per generation, which would only be realized in the absence of mutation, selection and immigration not exceeding 1 breeding individual per generation.

A Population in Stable Equilibrium

Introduction. Population size and population stability are 2 separate but related phenomena that deserve consideration in relation to processes we observed in this population. Our data provided some insight into possible mechanisms of stability, but did not address why the population contained about 200 individuals. We did demonstrate a significant correlation between dispersion of deer and dispersion of woody cover and, therefore, believe that population size was ultimately determined by number, size and dispersion of woodlots, which were surrounded by pastures containing nutritious forage. It seems plausible that the capacity of the study area to support deer actually increased from 1939-72 (see Table 1), in response to an increase in the ratio of high quality forage areas to closed areas of woody vegetation. This is reasonable given the apparent suitability of the "forest-edge" to white-tailed deer in North America (Severinghaus and Cheatum 1956). We do not know, however, what the optimum ratio and dispersion of open and closed areas should be on the Refuge to maintain a population of any given size.

Since we had no evidence that immigration was an important factor, natality was the only method of adding deer to this population. There were several proximate causes of mortality that removed deer from the population; data on movements indicated that emigration was negligible. Total mortality of yearlings and adults apparently balanced the number of fawns recruited annually from 1972-77. Correlation analysis suggested a negative feedback response between population size and the following year's recruitment of fawns into the population. Although Teer et al. (1965:41) found a significant inverse relationship between population density and reproduction (i.e., ovulation and conception rates) in white-tailed deer in Texas, variations in reproductive rate within populations of ungulates have not been proven to be density-dependent, according to Sinclair (1974:170). Regardless of the exact mechanism responsible for the relationship we observed, the effect would be a stabilization of population size at some level.

In Caughley's (1976) provocative discussion of ungulate population dynamics, he stated that there were 3 possible outcomes to which a vegetation-herbivore system might accede: unstable equilibrium, stable limit cycle, or stable equilibrium. He considered unstable equilibria and stable limit cycles, while theoretically possible, unlikely for ungulates; the "interaction of ungulates and vegetation typically leads to stable equilibrium through eruption and dampened oscillations" (1976:214). The reasoning Caughley used to arrive at this conclusion (1976:215) can be succinctly stated: natural selection has acted, both, against populations with a predilection toward limit cycles or unstable equilibria and against individuals in such populations, so that populations of these types are no longer extant. Available data for the population of CWTB on the Refuge mainland indicated that it was currently at stable equilibrium; whether it experienced any eruption or violent oscillations in the past is not known.

Hypotheses of food limitation. The major underlying assumption of Caughley's paper, although never explicitly stated, is that the density and response of an ungulate population to its environment is finely tuned to the amount of food available to each individual. That is, carrying capacity (K) is determined solely by availability of forage. Similarly, Klein (1965) documented correlations between quality and quantity of forage and certain population characteristics of Odocoileus and hypothesized a causal relationship. Low fawn production, delayed sexual maturation, a preponderance of older deer in the population, and a sex ratio favoring females due to heavy mortality of males were correlated with "poor" range. The opposite population characteristics were thought to result from "good" range. Following the reasoning of Caughley and Klein and based on known characteristics of the CWTB population we examined, we should conclude that population growth was limited by food availability and that habitat on the Refuge was of poor quality for these deer.

However, the density and stability of this population, the apparent availability of high quality herbaceous forage throughout the year,

and the general physical condition of the deer contradict these conclusions: 1) Refuge habitat was capable of consistently maintaining a whitetail population of approximately 25/km² and, therefore, should not be termed "poor." 2) A preliminary examination of rumen contents from 33 carcasses found during all seasons revealed that herbaceous vegetation had been ingested to the virtual exclusion of browse; short, green herbaceous vegetation was abundant on the area throughout the year; and, chemical analyses of 1 herbaceous species utilized by CWTB on the Refuge indicated its high quality with respect to protein content and digestibility. 3) The physical condition of 5 adults illegally shot on 23 February 1975 was very good. These deer were the closest approximation to a random sample from the "living" that we obtained during the study. 4) The physical condition of most carcasses found, as reflected in fat content of femur marrows from 65 yearling and adult deer, did not implicate malnutrition as the cause of death.

If food was not the major limiting factor in this population, several agents of mortality remain that could have prevented the herd from increasing: parasites, diseases, accidents and predators. We demonstrated that each of these factors was responsible for the death of certain individuals in the population; the relative contribution of each factor to total mortality was not really important. In fact, more than 1 critical mortality factor may have acted together (Lack 1954:276). The interesting question is: what was the nature of the mechanism that balanced mortality and recruitment, resulting in a population that was quite stable relative to its biotic potential?

Hypothesis of population stability. We hypothesize that the stability of this population ultimately derived from the constancy of the habitat and a relatively mild physical environment. This is not a new idea. Klein (1968:365) wrote:

There appears to be a relationship between the self-regulatory ability of animal populations and the relative stability of the environments within which they have evolved. For example, the North American deer [*Odocoileus*] that are adapted to early successional stages of vegetation, which are of a transitory nature, appear not to have well developed

self-regulatory mechanisms and are characterized by wide population fluctuations. On the other hand the roe deer (Capreolus capreolus) in Europe (Andersen 1963) and some bovids, such as the Uganda kob (Adenota kob thomasi) (Buechner 1963), that are found on relatively stable vegetation types, appear to have evolved behavioral mechanisms that tend to contribute to the stability of their populations.

However, it does not necessarily follow from Klein's generalization that because populations of Odocoileus fluctuate widely in habitats with low temporal permanence, that populations of the same species found in more constant habitats will also exhibit wide fluctuations. Our data on this population of CWTD establish that populations of virginianus are not invariably unstable. Since white-tailed deer are found in a wide variety of habitats of varying permanence from Canada to South America, one would expect to find a variety of strategies by individuals (the effect of which may result in population stability) across the species' geographic distribution in response to the environment inhabited. The fact that virginianus' geographic distribution is so large demands such an explanation.

Sedentary-agonistic females. On our study area, agricultural practices have maintained plant succession at an early seral stage for several decades, an event that could never be accomplished in such a productive environment for plant growth solely by the grazing pressure of ungulates native to the Pacific Northwest--black-tailed deer, Roosevelt elk and white-tailed deer. The habitat-environmental regime in southwestern Washington would have favored individuals with tactics best suited to an area with a constant supply of adequate forage. (Actually, forage availability would have been increasing gradually with the conversion of woodlots to pastures). The sedentary nature of adult females could be such a tactic. Once the habitat became stable, albeit due to man's agricultural practices, there would be no necessity for deer to migrate or to occupy large home ranges within which an individual could move as local conditions deteriorated. The most efficient strategy would be to remain on a familiar piece of range large enough to provide adequate cover and forage. Such a strategy could provide

benefits to the individual, due to its familiarity with a relatively small tract of land, that might include lower risk of physical injury during movements, increased efficiency at evading and escaping predators that chase their prey (e.g., wolf), and increased foraging efficiency. If females that displayed such a tactic experienced increased reproductive fitness relative to females that were not sedentary, and if this behavior was heritable, then this tactic could have become the norm for the population via natural selection that favored the sedentary genotype.

Concurrent with the increase of the sedentary strategy, females that were also capable of preventing other deer from utilizing the resources of the former's home range could increase their reproductive success relative to non-sedentary females even more. Spatial exclusion of conspecifics could be enforced by agonistic encounters similar to those we observed in this population. Even though the energetic costs of maintaining exclusive use over one's entire home range might be prohibitive, the defensibility of a portion of one's home range (e.g., bed site) might be economical enough to be profitable (Brown 1964). Agonistic interactions between females may have been common before females became sedentary, having developed in response to intraspecific competition for limited resources. The later application of such interactions to a resource that was spatially fixed within the home range of a sedentary female (i.e., bed site), and resulting in the exclusive use of that resource by the resident female, would constitute territoriality.

The origination of agonistic behavior in a population has been used as an example of an evolutionarily stable strategy (ESS) (Dawkins 1976), where strategy was defined as we have used it here: a pre-programmed behavioral policy. If the advantages we hypothesized actually existed for a sedentary female, then we see no reason why sedentari-ness in females could not have become an ESS. Dawkins (1976:74) defined an ESS as a strategy which, if most members of a population adopt it, can not be bettered by an alternative strategy. If females that displayed sedentary behavior were favored in a constant environment, then such a strategy could have spread rapidly through the population,

become an ESS, and will probably remain so until a major environmental change favors a different strategy.

Once a sedentary-agonistic strategy became an ESS and all available habitat became filled by whitetails, females would be committed to it and the consequences of local habitat deterioration. This might explain the reduction in deer density in unit R4, which was apparently due mainly to mortality of females in that area of the Refuge (see Spatial distribution of mortalities). A major reduction in haying and cattle grazing in this unit in 1972, where approximately 25% of the entire herd was found on 10% of the Refuge acreage, was continued through 1975. Although the exact mechanism inducing mortality of females was not known, our subjective analysis of forage conditions that was presented earlier suggested a decrease in availability of high quality forage. It would seem, then, that a CWT female was "locked in" to her established home range, even when its suitability diminished. Adult males, which were socially dominant over other sex-age classes in this population as elsewhere (Hirth 1977:35), were apparently free to move wherever they wanted. Because of this, they would not be as affected by local changes in habitat quality on the Refuge as would females.

Selection for dispersal distance. Constancy of habitat may also affect certain social features within a population. If we assume that the current absence of CWT from upland habitat adjacent to the river bottomland reflects an inability to survive there (whether due to habitat characteristics and/or the presence of dense populations of black-tailed deer), then there would have been strong selection against dispersers who left the riparian community. Although the exact vegetational composition of low elevation, flood-plain habitat along the Columbia River and its major tributaries was probably spatially and temporally variable in pre-settlement times, the patchy distribution and persistence of these riverine communities in the Pacific Northwest must have been stable in a general sense. The high cliff embankments currently found along much of the Columbia River would not have supported a riparian community in recent geologic time, for example. Conversely, land adjacent to the river below 3-5 m above sea level could

support only riparian vegetation, due to periodic flooding and tidal influences as far upriver as the present city of Portland. Once this habitat became filled with white-tailed deer, the chances of a dispersing individual locating suitable, unoccupied habitat and successfully reproducing would have been even lower than remaining near the natal area. This selection pressure was probably operating on this population of CMTD for a long time. This is the same reasoning used by Geist (1971) to explain dispersal patterns in other ungulates. He theorized that a fluctuating habitat was responsible for dispersal of juveniles in moose (Alces alces), while the stable habitat where bighorn sheep live favored integration of juveniles into the band. The historical stability of the habitat where whitetails currently exist could have a major influence on whether individuals of that population (or subspecies) are good or poor colonizers. We suggest that dispersal is strongly influenced by the environmental history in a population's geographic area; that is, virginianus does not exhibit a consistent species-wide pattern with regard to dispersal.

Although not exactly the same, it seems plausible that selection against long-distance dispersal that might end in unfavorable habitat and selection for a sedentary nature (in females) after establishment of home range would be complementary. For females, this resulted in individuals that were sedentary throughout their lives, beginning at birth. Even males did not exhibit dispersal off the Refuge, although it appeared they gradually left their natal area to establish home ranges elsewhere on the study area by 2 years of age. In fact, there seemed to be some attraction of males to the western end of the Refuge as reflected in shifts of centers of activity by several marked males as they matured (Fig. 15). Unfortunately, because of loss of collars or mortality we were unable to follow males marked as fawns until adulthood to solidly substantiate this.

Differential control of yearlings and adults by sex. Our hypothesis, then, entails separate controls on the number of males and the number of females in this population. Females would have been indirectly limited by the number of available areas suitable for

establishment of home range. This would not actually limit the number of females in the population, but the number of female groups. For most of the year, these groups were probably composed of a female, her female relatives and any fawns born to those females that year. If the habitat became unsuitable for such a female group, each individual in the group would experience an increased probability of mortality due to a combination of factors. The number of females in such groups would then be a product of female longevity and the number of female fawns successfully produced by each adult in the group. By remaining with one's mother in the natal area, an efficient system of use and eventually inheritance of the dam's home range, along with any exclusive use of its resources, could develop. This process was well documented for 2 females on the Refuge. No. 31 gave birth to a female fawn in 1972, who was later marked as No. 17. They shared exactly the same home range until 1978, when No. 31 disappeared and presumably died. During 6 years of shared residence, this pair was nearly always seen grazing or bedded together except during the fawning season, when they avoided each other. They each successfully raised a minimum of 1 male fawn to yearling age during this time; these males were only occasionally observed in their dam's home range after reaching 1 year of age. No. 17 was still using the same area in November 1978.

As male fawns approached 1 year of age, they left the female group, probably due to agonistic interactions with the dam. Males increased their movements into unfamiliar areas on the Refuge until establishing residency in an area, usually joining an established group of older males. One might predict yearling males to be more vulnerable to mortality than yearling females, since females maintained social bonds with their dam after 1 year of age and remained in the same home range. From June 1974-December 1977 we located 14 natural mortalities of yearling males, but only 4 carcasses of yearling females. This is circumstantial evidence to support the benefits of remaining on a familiar tract of land (or remaining with one's mother), as we hypothesized earlier for sedentary females. Of the 14 yearling males found, at least 8 died of causes other than nutritional stress as

indicated by femur fat content; at least 2 probably died of stress related to poor physical condition. After joining a buck group, each male's probability of mortality was somewhat positively correlated with the number of males in the population, if we make an assumption: male stress during the breeding season increased with the number of males that competed for estrous females. This would be a negative feedback mechanism that affected males in the population irrespective of females.

Control of recruitment rate. Thus far, we have addressed only how mortality rates, mediated largely by behavior, could effect relative stability in the number of yearling and adult deer. However, mortality rate was highest among fawns, which annually reduced potential growth of the population significantly. As suggested by correlation analysis, how could population size during winter be inversely correlated with fawn survival the following summer, if not through some relationship between forage and physical condition of females? Coyote predation on fawns could provide the necessary mechanism.

We concluded earlier that at least 32% of the fawns found dead during 1975 were killed by coyotes and from June-November 1978, at least 8 of 25 (53%) deaths of radio-collared fawns on the Refuge were due to coyote predation (A. C. Clark, pers. comm.). (These are not estimates of coyote predation on all fawns, only minimum estimates of the percentage of dead fawns killed by coyotes). It is reasonable to assume there were more females in the population in summer following a winter with a high population estimate than a winter with a lower estimate and, therefore, more fawns were born in summer following a larger winter population. This results from the timing of female mortality, which was minimal during winter and spring, and from the consistent tertiary sex ratio in the population.

If coyotes killed a higher percentage of fawns when fawn density was higher, this would have resulted in the inverse relationship that we obtained between population size and recruitment. We do not know whether this actually occurred, but there is a theoretical basis for such a supposition. Holling (1959) found the "functional response" curve of 3 species of small mammal predators, whether derived from field

or laboratory data, to exhibit an initial S-shaped rise up to a constant, maximum consumption of prey by these predators. That is, the percentage of prey taken increased with increasing prey density up to some maximum rate. Furthermore, Holling (1959:311) stated that the only necessary condition for this factor to regulate prey numbers, "is a rise in per cent predation over some range of prey densities and an effective birthrate [of prey] that can be matched at some density by mortality from predators." During 1975, at least 5 different coyotes were found on the study area, enough predators on such a small area (790 ha) to influence mortality rates of fawns and match the birth rate of prey referred to by Holling. If rate of predation was significantly higher in years of higher fawn density, then the inversivity we observed could have resulted.

One other factor may have contributed to increased mortality by coyotes at higher fawn densities. As already stated, higher fawn densities would have occurred in years of higher overall population density. Increased density could easily have resulted in an increased encounter rate between young fawns that were hidden in fields of dense vegetation and older deer. The young of most cervid species exhibit a "hider" strategy when separated from the mother, an adaptation to reduce encounters with predators and conspecifics (Lent 1974). An inadvertent disturbance might induce a fawn to leave its bedded position. Young cervids often follow large moving objects of the appropriate size range (Lent 1974), including humans, and could wander away from the area where they were left by their dam. Subsequent movement and vocalization by the fawn would increase the probability of being located by coyotes. Coyotes were probably not dependent upon killing deer for food, since they were observed hunting rodents (Microtus) throughout the year and nearly every deer carcass was scavenged. However, they could easily switch to fawns once this prey became available.

Disturbance of fawns by other deer that led to increased predation would be a strong selection pressure favoring females who exhibited territoriality. Exclusion of deer from the fawn's general vicinity by the dam would be a logical extension from active antagonism toward deer

that approached the fawn-doe pair. This latter behavior was often observed by us and was observed in black-tailed deer (Miller 1974) and mule deer (Robinette 1966:345). In a species whose young are concealed after birth in an area where predators are abundant, detailed knowledge of the behavioral relationship between the fawn and other conspecifics might provide some interesting results.

Conclusion. The individual selection versus group selection controversy was treated in some detail by Williams (1966) and Wiens (1966) after publication of Wynne-Edwards' (1962) treatise. We differ from Caughley (1976), who explicitly stated the probability of population selection (as well as individual selection), from Klein (1968), who intimated that natural selection operated at the level of the population, and from numerous researchers who emphasized certain demographic and social characteristics of African ungulates as adaptive to the population or species (Buechner 1963, Estes 1974, Spinage 1974). Grubb (1974b:221) went so far as to consider increased male mortality among Soay sheep as altruistic and favored by natural selection. Although natural selection has acted upon individual CWTD phenotypes for a long period of time, changes in habitat on the study area due to agricultural practices may have resulted in recent ecological responses by existing phenotypes. While we formulated our hypothesis of the sedentary female in terms of natural selection, this phenomenon may be a prime example of the interplay between long-term selection and short-term ecological response by an individual. Selection probably favored short-dispersers versus long-dispersers given the historical, patchy distribution of white-tailed deer habitat along the Columbia River. However, those same individuals fine-tuned their response to habitat found on the study area by exhibiting extreme sedentariness. That is, females were not inherently as sedentary as they behaved; if transplanted to an entirely different habitat, they may have exhibited longer movements and had larger home ranges. We believe, unequivocally, that the characteristics observed for this population can be "explained" by the behavior and ecology of individual deer. Concentrating on the tactics employed by

individual organisms may be a necessary and fruitful approach to understanding mechanisms (though subtle and perhaps cryptic) that influence population stability.

LITERATURE CITED

- ALEXANDER, B. G. 1968. Movements of deer in northeast Texas. *J. Wildl. Manage.*, 32(3):618-620.
- ALLEN, E. O. 1968. Range use, foods, condition and productivity of white-tailed deer in Montana. *J. Wildl. Manage.*, 32(1):130-141.
- ANDERSEN, J. 1963. Populations of hare and roe-deer in Denmark. *Proc. 16th Internat. Congr. Zool.*, 3:347-351.
- ANDERSON, E. W. and R. J. SCHERZINGER. 1975. Improving quality of winter forage for elk by cattle grazing. *J. Range Manage.*, 28(2): 120-125.
- ANTHONY, R. G. and N. S. SMITH. 1977. Ecological relationships between mule deer and white-tailed deer in southeastern Arizona. *Ecol. Monog.*, 47:255-277.
- AOAC. 1970. Official methods of analysis. 11th ed. Ass. Official Analytical Chemists. Wash., D.C. 1115pp.
- BELL, R. H. V. 1970. The use of the herb layer by grazing ungulates in the Serengeti. Pp. 111-124, in A. Watson (ed.), *Animal populations in relation to their food resources*. Blackwell Sci. Pub. Oxford. 477pp.
- BROWN, B. A., Jr. 1974. Social organization in male groups of white-tailed deer. Pp. 436-446, in V. Geist and F. Walther (eds.), *The behaviour of ungulates and its relation to management*. IUCN Pub. New Series No. 24. Vol. 1. 511pp.
- BROWN, J. L. 1975. *The evolution of behavior*. W. W. Norton and Co., Inc. New York. 761pp.
- BUECHNER, H. K. 1963. Territoriality as a behavioral adaptation to environment in Uganda kob. *Proc. 16th Internat. Congr. Zool.*, 3: 59-63.
- BYFORD, J. L. 1969. Movement responses of white-tailed deer to changing food supplies. *Proc. SE Assoc. Game and Fish Comm.*, 23:63-78.
- CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. Pp. 183-246, in T. H. Coaker (ed.), *Applied Biology*. Vol. 1. Academic Press. London. 358pp.
- CAUGHLEY, G. 1977. *Analysis of vertebrate populations*. John Wiley and Sons. London. 234pp.
- CHAPMAN, D. G. and W. S. OVERTON. 1966. Estimating and testing differences between population levels by the Schnabel estimation method. *J. Wildl. Manage.*, 30(1):173-180.
- COBLENTZ, B. E. 1970. Food habits of George Reserve deer. *J. Wildl. Manage.*, 34(3):535-540.

- COOK, R. S., M. WHITE, D. O. TRAINER and W. C. GLAZENER. 1971. Mortality of young white-tailed deer fawns in south Texas. *J. Wildl. Manage.*, 35(1):47-56.
- COWAN, I. McT. 1950. Some vital statistics of big game on overstocked mountain range. *Trans. 15th N.A. Wildlife Conf.*, 25:581-588.
- COWAN, R. L., J. S. JORDAN, J. L. GRIMES and J. D. GILL. 1970. Comparative nutritive values of forage species. Pp. 48-56, in *Range and wildlife habitat evaluation - A research symposium*. USDA Misc. Pub. No. 1147. 220pp.
- CROW, J. F. 1954. Breeding structure of populations. II. Effective population number. In, O. Kempthorne et al. (eds.), *Statistics and mathematics in biology*. Hafner. New York.
- CROW, J. F. and N. E. MORTON. 1955. Measurement of gene frequency drift in small populations. *Evol.*, 9:202-214.
- DAPSON, R. W. 1971. Quantitative comparison of populations with different age structures. *Ann. Zool. Fennici*, 8:75-79.
- DAPSON, R. W. 1972. Age structure of six populations of old-field mice, Peromyscus polionotus. *Res. Popul. Ecol.*, 13:161-169.
- DASMANN, R. F. and R. D. TABER. 1956. Behavior of Columbian black-tailed deer with reference to population ecology. *J. Mammal.*, 37(2):143-164.
- DAWKINS, R. 1976. *The selfish gene*. Oxford U. Press. New York. 224pp.
- DOUGLAS, D. 1829. Observations on two undescribed species of North American mammalia (Cervus leucurus et Ovis californianus). *Zool. J.*, 4:330-332.
- DOUGLAS, D. 1914. *Journal kept by David Douglas during his travels in North America 1823-1827*. W. Wesley and Son. London. 364pp.
- DOWNING, R. L. and B. S. MCGINNES. 1969. Capturing and marking white-tailed deer fawns. *J. Wildl. Manage.*, 33(3):711-714.
- DOWNING, R. L., E. D. MICHAEL and R. J. POUX, Jr., 1977. Accuracy of sex and age ratio counts of white-tailed deer. *J. Wildl. Manage.*, 41(4):709-714.
- ESTES, R. D. 1974. Social organization of the African Bovidae. Pp. 166-205, in V. Geist and F. Walther (eds.), *The behaviour of ungulates and its relation to management*. IUCN Pub. New Series No. 24. Vol. 1. 511pp.
- FLOOK, D. R. 1970. A study of sex differential in the survival of wapiti. *Can. Wildl. Serv. Rep. Series No. 11*. 71pp.
- FRANKLIN, J. F. and C. T. DYRNESS. 1973. *Natural vegetation of Oregon and Washington*. USDA For. Serv. Gen. Tech. Rep. PNW-8. 417pp.

- FRENCH, C. E., L. C. McEWEN, N. D. MAGRUDER, R. H. INGRAM and R. W. SWIFT. 1955. Nutritional requirements of white-tailed deer for growth and antler development. Pa. St. U. AES Bull. 600. 50pp.
- GAVIN, T. 1978. Status of the Columbian white-tailed deer: Some quantitative uses of biogeographic data. Pp. 185-202, in Threatened deer. IUCN. Morges, Switzerland. 434pp.
- GAVIN, T. A. (in press). The Columbian white-tailed deer. In, L. K. Halls (ed.), Ecology and management of white-tailed deer. The Stackpole Co. Harrisburg.
- GEIST, V. 1971. Mountain sheep. U. of Chicago Press. Chicago. 383pp.
- GREER, K. R. 1968. A compression method indicates fat content of elk (Wapiti) femur marrows. J. Wildl. Manage., 32(4):747-751.
- GRUBB, P. 1974a. Population dynamics of the Soay sheep. Pp. 242-272, in P. A. Jewell, C. Milner and J. M. Boyd (eds.), Island survivors: The ecology of the Soay sheep of St. Kilda. The Athlone Press. London. 386pp.
- GRUBB, P. 1974b. The rut and behavior of Soay rams. Pp. 195-223, in P. A. Jewell, C. Milner and J. M. Boyd (eds.), Island survivors: The ecology of the Soay sheep of St. Kilda. The Athlone Press. London. 386pp.
- GRUBB, P. and P. A. JEWELL. 1974. Movement, daily activity and home range of Soay sheep. Pp. 160-194, in P. A. Jewell, C. Milner and J. M. Boyd (eds.), Island survivors: The ecology of the Soay sheep of St. Kilda. The Athlone Press. London. 386pp.
- GUNVALSON, V. E., A. B. ERICKSON and D. W. BURCALOW. 1952. Hunting season statistics as an index to range conditions and deer population fluctuations in Minnesota. J. Wildl. Manage., 16(2):121-131.
- HARDER, J. D. and T. J. PETERLE. 1974. Effect of diethylstilbestrol on reproductive performance of white-tailed deer. J. Wildl. Manage., 38(2):183-196.
- HARDIN, J. W., N. J. SILVY and W. D. KLIMSTRA. 1976. Group size and composition of the Florida Key deer. J. Wildl. Manage., 40(3):454-463.
- HAWKINS, R. E. and W. D. KLIMSTRA. 1970. A preliminary study of the social organization of white-tailed deer. J. Wildl. Manage., 34(2):407-419.
- HAWKINS, R. E., W. D. KLIMSTRA and D. C. AUTRY. 1971. Dispersal of deer from Crab Orchard National Wildlife Refuge. J. Wildl. Manage., 35(2):216-220.
- HEPTNER, W. G., A. A. NASIMOVITSCH and A. G. BANNIKOV. 1961. Mammals of the Soviet Union. German translation. Jena:VEB Gustav Fischer-Verlag.
- HIRTH, D. H. 1977. Social behavior of white-tailed deer in relation to habitat. Wildl. Monog. No. 53. 55pp.

- HITCHCOCK, C. L. and A. CRONQUIST. 1973. Flora of the Pacific Northwest. U. of Wash. Press. Seattle. 730pp.
- HOLLING, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *The Can. Ent.*, 91:293-320.
- HOSLEY, N. W. 1956. Management of the white-tailed deer in its environment. Pp. 187-259, in W. P. Taylor (ed.), *The deer of North America*. The Stackpole Co. Harrisburg. 668pp.
- HOWARD, W. E. 1960. Innate and environmental dispersal of individual vertebrates. *Amer. Midl. Nat.*, 63:152-161.
- JENNRICH, R. I. and F. B. TURNER. 1969. Measurement of non-circular home range. *J. Theoret. Biol.*, 22:227-237.
- KAMMERMEYER, K. E. and R. L. MARCHINTON. 1976. The dynamic aspects of deer populations utilizing a refuge. *Proc. SE Assoc. Game and Fish Comm.*, 29:466-475.
- KIRKPATRICK, C. M., C. M. WHITE, T. W. HOEKSTRA, F. A. STORMER and H. P. WEEKS, Jr. 1976. White-tailed deer of US Naval Ammunition Depot Crane. *Purdue U. AES Res. Bull. No. 932*. 42pp.
- KLEIN, D. R. 1965. Ecology of deer range in Alaska. *Ecol. Monog.*, 35(3):259-284.
- KLEIN, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. *J. Wildl. Manage.*, 32(2):350-367.
- KLEIN, D. R. and S. T. OLSON. 1960. Natural mortality patterns of deer in southeast Alaska. *J. Wildl. Manage.*, 24(1):80-88.
- LACK, D. 1954. *The natural regulation of animal numbers*. Oxford U. Press. Oxford. 343pp.
- LAUCKHART, J. B. 1940. Washington Dept. of Game Rep. Mimeo. 3pp.
- LENT, P. C. 1974. Mother-infant relationships in ungulates. Pp. 14-55, in V. Geist and F. Walther (eds.), *The behaviour of ungulates and its relation to management*. IUCN Pub. New Series No. 24. Vol. 1. 511pp.
- LINDZEY, F. G. and E. C. MESLOW. 1972. Developments in wildlife age determination exemplified by the black bear. *Proc. 52nd Ann. Conf. Western Assoc. Game and Fish Comm.*, 295-307.
- LONGHURST, W. M., H. K. OH, M. B. JONES and R. E. KEPNER. 1968. A basis for the palatability of deer forage plants. *Trans. 33rd N.A. Wildl. Conf.*, 181-192.
- MAGRUDER, N. D., C. E. FRENCH, L. C. McEWEN and R. W. SWIFT. 1957. Nutritional requirements of white-tailed deer for growth and antler development. II. Experimental results of the third year. *Pa. St. U. AES Bull. No. 628*. 21pp.

- MARSHALL, A. D. and R. W. WHITTINGTON. 1968. A telemetric study of deer home ranges and behavior of deer during managed hunts. Proc. S.E. Assoc. Game and Fish Comm., 22:30-46.
- MAYR, E. 1963. Populations, species and evolution. The Belknap Press. Cambridge. 453pp.
- MCCAFFERY, K. R., J. TRANETZKI and J. PIECHURA, Jr. 1974. Summer foods of deer in northern Wisconsin. J. Wildl. Manage., 38(2):215-219.
- MCCULLOUGH, D. R. 1969. The Tule elk: Its history, behavior and ecology. U. of Cal. Pub. Zool. V. 88. 209pp.
- MCNAUGHTON, S. J. 1976. Serengeti migratory wildebeest: Facilitation of energy flow by grazing. Sci., 191:92-94.
- MECH, L. D. and L. D. FRENZEL, Jr. 1971. An analysis of the age, sex, and condition of deer killed by wolves in northeastern Minnesota. Pp. 35-51, in L. D. Mech and L. D. Frenzel, Jr. (eds.), Ecological studies of the timber wolf in northeastern Minnesota. USDA For. Serv. Res. Paper NC-52. 62pp.
- MICHAEL, E. D. 1965. Movements of white-tailed deer on the Welder Wildlife Refuge. J. Wildl. Manage., 29(1):44-52.
- MILLER, F. L. 1974. Four types of territoriality observed in a herd of black-tailed deer. Pp. 644-660, in V. Geist and F. Walther (eds.), The behaviour of ungulates and its relation to management. IUCN Pub. New Series No. 24. Vol. 2. 428pp.
- MOEN, A. N. 1973. Wildlife ecology. W. H. Freeman and Co. San Francisco. 458pp.
- MOHLER, L. L., J. H. WAMPOLE and E. FICHTER. 1951. Mule deer in Nebraska National Forest. J. Wildl. Manage., 15(2):129-157.
- MURIE, O. J. 1930. An epizootic disease of elk. J. Mammal., 11:214-222.
- MURPHY, D. A. and J. A. COATES. 1966. Effects of dietary protein on deer. Trans. 31st N.A. Wildl. Conf., 31:129-139.
- NAGY, J. G., T. HAKONSON and K. L. KNOX. 1969. Effects of quality on food intake in deer. Trans. 34th N.A. Wildl. Conf., 34:146-154.
- NEILAND, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. J. Wildl. Manage., 34(4):904-907.
- O'PEZIO, J. P. 1978. Mortality among white-tailed deer fawns on the Seneca Army Depot. N.Y. Fish and Game J., 25(1):1-15.
- OVERTON, W. S. 1971. Estimating the numbers of animals in wildlife populations. Pp. 403-455, in R. H. Giles, Jr. (ed.), Wildlife management techniques. 3rd ed. The Wildlife Society. Wash., D.C. 623pp.
- PARKE, DAVIS and COMPANY. 1974. Veterinary Medical summary. Parke, Davis and Co. Ann Arbor. 76pp.

- PROGULSKE, D. R. and T. S. BASKETT. 1958. Mobility of Missouri deer and their harassment by dogs. *J. Wildl. Manage.*, 22(2):184-192.
- RANSOM, A. B. 1967. Reproductive biology of white-tailed deer in Manitoba. *J. Wildl. Manage.*, 31(1):114-123.
- RICE, W. R. and J. D. HARDER. 1977. Application of multiple aerial sampling to a mark-recapture census of white-tailed deer. *J. Wildl. Manage.*, 41(2):197-206.
- ROBINETTE, W. L. 1966. Mule deer home range and dispersal in Utah. *J. Wildl. Manage.*, 30(2):335-349.
- ROBINETTE, W. L., J. S. GASHWILER, J. B. LOW and D. A. JONES. 1957. Differential mortality by sex and age among mule deer. *J. Wildl. Manage.*, 21(1):1-16.
- ROSEBERRY, J. L. and W. D. KLIMSTRA. 1970. Productivity of white-tailed deer on Crab Orchard National Wildlife Refuge. *J. Wildl. Manage.*, 34(1):23-28.
- ROSEN, M. N. 1970. Necrobacillosis. Pp. 286-292, in J. W. Davis, L. H. Karstad and D. O. Trainer (eds.), *Infectious diseases of wild mammals*. Iowa St. U. Press. Ames. 421pp.
- ROSEN, M. N., O. A. BRUNETTI, A. I. BISCHOFF and J. A. AZEVEDO. 1951. An epizootic of foot rot in California deer. *Trans. 16th N.A. Wildl. Conf.*, 16:164-178.
- SANDERSON, G. C. 1966. The study of mammal movements - A review. *J. Wildl. Manage.*, 30(1):215-235.
- SCHEFFER, V. B. 1940. A newly located herd of Pacific white-tailed deer. *J. Mammal.*, 21(3):271-282.
- SEGELQUIST, C. A., H. L. SHORT, F. D. WARD and R. G. LEONARD. 1972. Quality of some winter deer forages in the Arkansas Ozarks. *J. Wildl. Manage.*, 36(1):174-177.
- SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *J. Wildl. Manage.*, 13(1):195-216.
- SEVERINGHAUS, C. W. and E. L. CHEATUM. 1956. Life and times of the white-tailed deer. Pp. 57-186, in W. P. Taylor (ed.), *The deer of North America*. The Stackpole Co. Harrisburg. 668pp.
- SINCLAIR, A. R. E. 1974. The natural regulation of buffalo populations in East Africa. I. Introduction and resource requirements. *E. Afr. Wildl. J.*, 12:135-154.
- SINCLAIR, A. R. E. 1974. The natural regulation of buffalo populations in East Africa. II. Reproduction, recruitment and growth. *E. Afr. Wildl. J.*, 12:169-183.
- SKINNER, W. R. and E. S. TELFER. 1974. Spring, summer and fall foods of deer in New Brunswick. *J. Wildl. Manage.*, 38(2):210-214.
- SOKAL, R. R. and F. J. ROHLF. 1969. *Biometry*. W. H. Freeman and Co. San Francisco. 776pp.

- SOTALA, D. J. and C. M. KIRKPATRICK. 1973. Foods of white-tailed deer, Odocoileus virginianus, in Martin County, Indiana. Amer. Midl. Nat., 89(2):281-286.
- SPIESS, E. B. 1977. Genes in populations. John Wiley and Sons, Inc. New York. 780pp.
- SPINAGE, C. A. 1974. Territoriality and population regulation in the Uganda defassa waterbuck. Pp. 635-643, in V. Geist and F. Walther (eds.), The behaviour of ungulates and its relation to management. IUCN Pub. New Series No. 24. Vol. 2. 428pp.
- STEEL, R. G. D. and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co. New York. 481pp.
- STORMER, F. A. 1972. Population ecology and management of white-tailed deer of Crane Naval Ammunition Depot. Ph.D. Thesis. Purdue U. 274pp.
- STRANDGAARD, H. 1972. The roe-deer (Capreolus capreolus) population at Kalø and the factors regulating its size. Dan. Rev. Game Biol., Vol. 7, No. 1. 205pp.
- STRUHSAKER, T. T. 1967. Behavior of elk (Cervus canadensis) during the rut. Zeit. für Tierpsy., 24(1):80-114.
- SURING, L. H. 1974. Habitat use and activity patterns of the Columbian white-tailed deer along the lower Columbia River. M.S. Thesis. Oregon St. U. Corvallis. 59pp.
- SURING, L. H. and P. A. VOHS, Jr. (in press). Habitat use by Columbian white-tailed deer. J. Wildl. Manage.
- SWIFT, R. W. 1948. Deer select most nutritious forages. J. Wildl. Manage., 12(1):109-110.
- TABER, R. D. and R. F. DASMANN. 1954. A sex difference in mortality in young Columbian black-tailed deer. J. Wildl. Manage., 18(3):309-315.
- TEER, J. G., J. W. THOMAS and E. A. WALKER. 1965. Ecology and management of white-tailed deer in the Llano Basin of Texas. Wildl. Monog. No. 15. 62pp.
- THOMAS, J. W., R. M. ROBINSON and R. G. MARBURGER. 1965. Social behavior in a white-tailed deer herd containing hypogonadal males. J. Mammal., 46(2):314-327.
- THOMAS, J. W., J. G. TEER and E. A. WALKER. 1964. Mobility and home range of white-tailed deer on the Edwards Plateau in Texas. J. Wildl. Manage., 28(3):463-472.
- THWAITES, R. G., (ed.). 1905. Original journals of the Lewis and Clark expedition, 1804-1806. Dodd, Mead and Co. New York. Vol. 4. 363pp.
- TILLEY, J. M. A. and R. A. TERRY. 1963. A two stage technique for the in vitro digestion of forage crops. J. Brit. Grass. Soc., 18:104-111.

- ULLREY, D. E., W. G. YOUATT, H. E. JOHNSON, L. D. FAY and B. L. BRADLEY. 1967. Protein requirement of white-tailed deer fawns. *J. Wildl. Manage.*, 31(4):679-685.
- VAUGHAN, T. A. 1972. *Mammalogy*. W. B. Saunders Co. Philadelphia. 463pp.
- VERME, L. J. 1967. Influence of experimental diets of white-tailed deer reproduction. *Trans. 32nd N.A. Wildl. Conf.*, 405-420.
- VERME, L. J. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. *J. Wildl. Manage.*, 33(4):881-887.
- VERME, L. J. and J. C. HOLLAND. 1973. Reagent-dry assay of marrow fat in white-tailed deer. *J. Wildl. Manage.*, 37(1):103-105.
- WHITE, M. 1973. The whitetail deer of the Aransas National Wildlife Refuge. *Texas J. Sci.*, 24(4):457-489.
- WHITE, M., F. F. KNOWLTON and W. C. GLAZENER. 1972. Effects of dam-newborn fawn behavior on capture and mortality. *J. Wildl. Manage.*, 36(3):897-906.
- WHITEHEAD, G. K. 1972. *Deer of the world*. Constable and Co. London. 194pp.
- WIENS, J. A. 1966. On group selection and Wynne-Edwards' hypothesis. *Am. Sci.*, 54:273-287.
- WILLIAMS, G. C. 1966. *Adaptation and natural selection*. Princeton U. Press. Princeton. 307pp.
- WILSON, E. O. 1975. *Sociobiology*. The Belknap Press. Cambridge. 697pp.
- WILSON, E. O. and W. H. BOSSERT. 1971. *A primer of population biology*. Sinauer Associates, Inc. Stamford. 192pp.
- WOOD, A. J., I. McT. COWAN and H. C. NORDAN. 1962. Periodicity of growth in ungulates as shown by deer of the genus Odocoileus. *Can. J. Zool.*, 40:593-603.
- WRIGHT, J. F. 1958. Necrotic stomatitis in an American elk. *Vet. Med.*, 53(10):520-521.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behavior*. Oliver and Boyd. Edinburgh. 653pp.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall. Englewood Cliffs, N.J. 620pp.

APPENDIX

Appendix A. Common plants on the CWT National Wildlife Refuge
mainland.^a

COMMON NAME

SCIENTIFIC NAME

Trees

Sitka spruce	<u>Picea sitchensis</u>
Western red cedar	<u>Thuja plicata</u>
Red alder	<u>Alnus rubra</u>
Big-leaf maple	<u>Acer macrophyllum</u>
Indian plum	<u>Osmaronia cerasiformis</u>
Coast red elderberry	<u>Sambucus racemosa</u>
Red-osier dogwood	<u>Cornus stolonifera</u>
Willow	<u>Salix spp.</u>

Shrubs

Common snowberry	<u>Symphoricarpos albus</u>
Evergreen blackberry	<u>Rubus laciniatus</u>
Himalayan blackberry	<u>Rubus discolor</u>
Pacific blackberry	<u>Rubus ursinus</u>
Salmonberry	<u>Rubus spectabilis</u>
Rose	<u>Rosa sp.</u>
Coast black gooseberry	<u>Ribes divaricatum</u>

Herbaceous

Common cat-tail	<u>Typha latifolia</u>
Common rush	<u>Juncus effusus</u>
Sedge	<u>Carex sp.</u>
Canada thistle	<u>Cirsium arvense</u>
Creeping buttercup	<u>Ranunculus repens</u>
Siberian montia	<u>Montia sibirica</u>
Horsetail	<u>Equisetum sp.</u>
Sword fern	<u>Polystichum munitum</u>
Skunk cabbage	<u>Lysichitum americanum</u>
Clover	<u>Trifolium spp.</u>
Birdsfoot-trefoil	<u>Lotus corniculatus</u>
Smartweed	<u>Polygonum spp.</u>
Dock	<u>Rumex sp.</u>
Cow parsnip	<u>Heracleum lanatum</u>
Stinging nettle	<u>Urtica dioica</u>

Appendix A. continued.

Gramineae

Reed canarygrass	<u>Phalaris arundinacea</u>
Orchard-grass	<u>Dactylis glomerata</u>
Meadow foxtail	<u>Alopecurus pratensis</u>
Water foxtail	<u>Alopecurus geniculatus</u>
Common velvet-grass	<u>Holcus lanatus</u>
Tall fescue	<u>Festuca arundinacea</u>
Bentgrass	<u>Agrostis alba</u>
Italian ryegrass	<u>Lolium multiflorum</u>
English ryegrass	<u>Lolium perenne</u>

^aBotanical nomenclature followed Hitchcock and Cronquist (1973).

Appendix B. Status of all collared deer on the CWT National Wildlife Refuge mainland during February-March.^a

Deer #	Age-Sex ^b	1975		1976	
		Feb	Mar	Feb	Mar
1	Adult female	+	+	-	-
5	" "	+	+	+	+
10	" "	+	+	+	+
17	" "	+	+	+	+
23	" "	+	+	+	+
27	" "	+	+	+	+
31	" "	+	+	+	+
51	" "	+	+	+	+
55	" "	+	+	-	-
70	" "	+	+	-	-
7	" "	-	-	+	+
A3	" "	-	-	+	+
A4	" "	-	-	+	+
59	" "	-	-	+	+
22	Adult male	+	+	-	-
38	" "	+	+	-	-
60	" "	+	+	+	+
69	" "	+	+	-	-
88	" "	-	-	+	+
B2	" "	-	-	+	+
29	Yearling female	-	-	+	+
A7	" "	-	-	+	+
52	" "	+	+	+	+
54	" "	+	+	+	+
12	Yearling male	+	+	-	-
62	" "	+	+	-	-
83	" "	+	-	-	-
B1	" "	-	-	+	+
85	" "	-	-	+	+
57	Fawn female	+	+	-	-
53	" "	+	+	+	+
71	" "	+	+	+	+
28	" "	-	+	+	+
84	Fawn male	+	+	-	-
67	" "	+	+	-	-
86	" "	-	+	-	-
82	" "	+	+	+	+

^aPlus sign indicates deer was alive and collared in that month. Minus sign indicates deer was either dead or not collared in that month.

^bAges are for the earliest month in which a plus sign appears.

Appendix C. Procedure for obtaining data points used in ecological longevity curves, using ages at death for males as an example. (N=61, relative frequency=1/N, relative cumulative frequency (RCF) was accumulated from oldest to youngest).

<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>	<u>Age (yr)</u>	<u>RCF</u>
7.6	0.016	3.7	0.361	2.0	0.705
6.6	0.033	3.6	0.377	2.0	0.721
6.5	0.049	3.5	0.393	1.9	0.738
6.5	0.066	3.5	0.410	1.8	0.754
6.3	0.082	3.5	0.426	1.8	0.770
5.8	0.098	3.5	0.443	1.8	0.787
5.7	0.115	3.5	0.459	1.7	0.803
5.7	0.131	3.5	0.475	1.7	0.820
5.7	0.148	3.5	0.492	1.6	0.836
5.6	0.164	3.4	0.508	1.6	0.852
5.5	0.180	3.4	0.525	1.5	0.869
5.5	0.197	3.2	0.541	1.5	0.885
5.5	0.213	3.0	0.557	1.5	0.902
5.3	0.230	2.9	0.574	1.5	0.918
5.2	0.246	2.8	0.590	1.5	0.934
4.7	0.262	2.7	0.607	1.4	0.951
4.5	0.279	2.5	0.623	1.2	0.967
4.5	0.295	2.5	0.639	1.2	0.984
4.5	0.311	2.5	0.656	1.1	1.000
4.3	0.328	2.3	0.672		
4.0	0.344	2.3	0.689		
