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Correlation of white-tailed deer activity, distribution and behavior with climatic and other environmental factors

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FINAL

JOB COMPLETION REPORT

RESEARCH PROJECT SEGMENT

State of: New York

Project No. W-105-R-7

Job No. V-A

Name: Wildlife Habitat Improvement Investigations in the Central Adirondack Mountains

Title: Correlation of white-tailed deer activity, distribution and behavior with climatic and other environmental factors

Period Covered: April 1, 1966 - June 30, 1966

Abstract: A separate report, Behavior Of White-tailed Deer In An Adirondack Forest, was prepared. It contains details of procedures and findings.

The behavior of white-tailed deer (*Odocoileus virginianus borealis*, Miller) was studied on a 15,000-acre forest in the Adirondack Mountains from June, 1963 through February, 1966. Distribution and activity were investigated by counts of 24-hour accumulations of tracks on forest roads, and activity, ranging, social behavior, aquatic feeding behavior, and response to human disturbance were studied by observation of deer along roadsides and lakeshores.

Deer were uniformly distributed from May into November, except that from May through July local concentrations occurred where food or minerals occurred in concentrated abundance. Distribution from May through October was essentially independent of forest type, physiography, and changes in cover. The trend toward concentration in coniferous shelter types began in November, and during the winter and early spring areas with continuous coniferous overhead cover were favored by deer. The trend toward concentration was most closely associated with increasing frequency of occurrence of severe windchill in November and December, but once concentration was established, distribution was more closely associated with changes in the depth to which deer sank in the snow. Reduced use of coniferous shelter types from mid-March through April was associated with decreasing frequency of occurrence of severe windchill.

Slight differences were found in temperature and relative humidity within a wintering area, but differences in wind were great between exposed and sheltered locations. Wind was consistently least in the conifer type, where snow was somewhat shallower than in other types. Deer bedding was closely associated with the extent of coniferous crown cover in the different types, and bed sites were usually located in areas where the snow was shallower than average.

Limited observations of marked deer indicated that some animals

wintered on restricted portions of their summer-fall ranges, while others apparently wintered on distinctly different ranges. Summer movements varied considerably, with some individuals appearing quite sedentary, while others moved between one and two miles in less than 24 hours.

Activity was highest in May and June, intermediate in November (during the rut), and lowest in March and October. Mid-winter activity was variable, and could not be compared to that of other seasons due to restrictions on distribution.

From March through October 24-hour activity levels were significantly correlated with hours of daylight, but not with maximum daily temperature or minimum daily relative humidity. Thus, while 76 percent of the variation in activity was attributable to the three variables in combination, 74 percent was attributable to daylight length alone. Other correlation analyses for activity over the summer consistently confirmed the correlation between activity and daylight length. This correlation may be tentatively explained on the basis of the results of studies of captive white-tails which indicate the same general patterns for feed consumption and basal metabolism. Thus, the activity pattern observed is most likely the result of changes in light acting on the pituitary, with the resultant control of metabolism through the pituitary-thyroid axis.

Prolonged storms at any season resulted in lowered activity, although activity appeared to be increased immediately prior to, and during the early stages of snowstorms. In January and February 24-hour activity levels were positively correlated with maximum daily temperature, but not with other measures of temperature, relative humidity, wind, windchill, or snowdepth. In summer, relative humidity was negatively correlated with daytime activity at a lake. Daytime activity patterns indicated that midday summer temperatures were generally insufficient to depress deer activity. Nighttime activity in summer was more closely associated with weather prior to the spotlighting period than with weather during the counting period, but only temperature was significantly correlated (positively). No marked relationships were observed between deer activity and seasonal changes in food and cover, changes in abundance of biting flies, nor changes in human activity.

Throughout most of the summer most adult females were seen alone or with their newborn fawns, while yearlings were alone or with other yearlings. Adult males were either solitary, or associated almost exclusively with other adult males.

Deer use of a lake was found to be closely associated with the abundance, distribution, and condition of aquatic food plants, and not related to abundance of biting flies.

Deer appeared to react less markedly to disturbance by humans and vehicles in summer, than at other seasons. A broad trend of less pronounced response occurred from March through July, and reversed from July through the winter.

Recommendations: This job should be discontinued. Similar studies in other regions should be undertaken to provide more complete information on deer behavior. Detailed studies of the distribution patterns of deer in winter should be made to determine why deer seek shelter in winter, and if such shelter is simply preferred habitat, or is absolutely essential.

Objectives: The objectives of this job were: (1) to document daily and seasonal patterns of distribution; (2) to examine the relationship of environmental variables to distribution patterns; (3) to document daily and seasonal activity patterns; (4) to examine the relationship of environmental variables to activity patterns; (5) to examine the nature of distribution and activity patterns in relation to physiological-psychological changes in the deer (as determined in other studies); (6) to observe activity and ranging of individuals and to relate these observations to general patterns; (7) to observe social behavior and to relate it to seasonal patterns; (8) to observe the response of deer to human disturbance and to relate changes in this response to seasonal patterns.

Techniques Used: The details of the method of investigation are described in the report, Behavior Of White-tailed Deer In An Adirondack Forest.

Findings: The findings are given in the report, Behavior Of White-tailed Deer In An Adirondack Forest.

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TABLE OF CONTENTS

Page

CHAPTER III

CHAPTER IV

Page

CHAPTER V

CHAPTER VI

LIST OF TABLES

Table

Table

LIST OF FIGURES

Figure

Figure

BEHAVIOR OF WHITE-TAILED DEER IN AN ADIRONDACK FOREST

CHAPTER I

INTRODUCTION

"The white-tailed deer is one of the most beautiful animals on the North American continent. Its bouyancy in motion, grace in form and statuesque poise challenge our admiration." (Severinghaus, 1955). Thus, has one student of the white-tail (Odocoileus virginianus) expressed his admiration of the beauty of the deer. Equally as admirable is the great adaptability of the species which has allowed it to survive persecution in recent centuries (Young, 1956), and, with the aid of restrictive hunting regulations, to extend its range in spite of grossly changing environments. It is this great adaptability in particular, that challenges the student of animal behavior and ecology alike.

Scott (1958) differentiates between observational and experimental studies of behavior. In discussing observational studies he states (1958, p. 24):

> Relatively few species have ever been studied in more than a superficial manner, and the information is particularly important at the present time because of current interest and progress in the study of social behavior and organization. Each species which is studied in this fashion provides basic data for understanding the working of animal societies.

In the deer family (Cervidae), probably only Darling's (1937) study of the red deer (Cervus elaphus) is sufficient to be useful in this sense.

Scott (1958) cites three general reasons for studying the behavior of animals. These are: (1) human curiosity of the unknown; (2) relationship of behavior to economic problems; and, (3) the relationship of animal behavior to human behavior. He stresses that the application of sound knowledge of the behavioral characteristics of some animals to human affairs may be very useful, whereas application based upon erroneous or incomplete knowledge may be disastrous. In addition, sound basic information is required to intelligently manage valuable animals. The white-tailed deer is such an animal, and the benefits of proper management range from purely economic to entirely aesthetic. Forest managers, game managers, and parks managers may all be concerned. Thus, sound information on deer behavior should influence both the philosophy and technique of management in a truly positive manner. Management based on superficial knowledge, on the other hand, may result in complete failure, or, at best, prove to be much more complicated and expensive than is actually required.

A separate, final report for P-R Project W-105-R-7, Job V-A.

Scope Of The Study

In order to provide information on many phases of the annual behavior complex, this study was designed to measure behavior throughout the year. The principal study area was a 15,000-acre forest located in the center of the Adirondack Mountains of northern New York. The subject of the study, the northern woodland white-tailed deer (*Odocoileus virginianus borealis*, Miller), is described in the work of Kellogg (1956).

The major objectives of this study were the documentation of basic patterns of distribution and activity, and the relationship of selected environmental factors to these patterns. It should be clearly recognized, however, that this is essentially a study of behavior, and not an environmental analysis. While many environmental factors were measured, the primary objective was not to document them, but simply to relate them to behavior patterns.

As intimated above, there are two distinct types of behavioral studies. One seeks to *document* behavior, usually in natural, or at least semi-natural environments. Generally these are field studies in which systematic observation is the principal technique. The other kind of study seeks to *explain* behavior in terms of cause (stimulus) and effect (response). The latter are usually laboratory studies, and can hardly be approached intelligently for a species until a reasonable level of knowledge of what constitutes behavior in the natural environment has been attained. This study properly belongs in the category of the observational study in the natural, but not wilderness environment. The intent has been to document behavior in quantitative terms whenever possible, following the inductive method. Projections of results to suggest possible explanations of behavior have, by necessity, been restricted to deductive reasoning alone.

Objectives

To understand the objectives properly, the meaning of the terms "distribution" and "activity" should be made entirely clear. As used herein, these terms are defined as follows:

Distribution - the actual location of deer activity in the forest; especially important in relation to spatial environmental factors, i.e., forest type, aspect, etc.

Activity - the amount of deer activity within a given period of time as evidenced by tracks or sightings.

The major objectives of the study were:

(1) to document daily and seasonal patterns of distribution;

(2) to examine the relationship of environmental variables to distribution patterns;

(3) to document daily and seasonal activity patterns;

(4) to examine the relationship of environmental variables to activity patterns;

methodology in relation to anthropomorphism.

> I still go on the principle that if you are watching the higher animals, watch them as if they were human beings of a different civilization or culture, and if you are watching human beings observe them as if they were animals. Your anticipation of the next move will not be far wrong. You are still left with plenty of room for the most profound scientific thinking and research to arrive at the origins and inter-relationships of behaviour. It is best to stop being anthropomorphic then.

CHAPTER II

METHOD OF INVESTIGATION

The Study Area

The study area was The Archer and Anna Huntington Wildlife Forest Station, a 15,000-acre property owned by Syracuse University, and operated by the State University College of Forestry for the purpose of conducting wildlife research. A detailed account of the early history of the Forest is presented in King, et al. (1941). More recent developments are summarized in annual reports of Forest activities (Patric, unpub. reports, 1959-1965).

Important physical facilities of the Forest include work buildings, residences, wheeled and tracked vehicles, and a road system of about 18 miles. A permanently-marked, quarter-mile grid system covers most of the Forest, and provides excellent ground control.

The Huntington Forest is located approximately five miles northwest of the village of Newcomb, near the center of the Adirondack Mountains of northern New York. This is also near the center of the Adirondack Game Range Division described by Smith (1955).

Physiography

Smith (1955) characterizes the Adirondack Division as mountainous, with elevations generally ranging from about 1,000 feet to well over 5,000 feet. Heady (1940, p. 238) summarizes the topography and drainage of the Huntington Forest as follows:

> Surrounded by the highest peaks of the Adirondacks on the north and northeast, and by only slightly lower mountains to the west, south, and east, the Forest has an average elevation of 1800 to 2000 feet above

(5) to examine the nature of distribution and activity patterns in relation to physiological-psychological changes in the deer (as determined in other studies);

(6) to observe activity and ranging of individuals and to relate these observations to general patterns;

(7) to observe social behavior and to relate it to seasonal patterns;

(8) to observe the response of deer to human disturbance and to relate changes in this response to seasonal patterns.

Some Additional Considerations In The Study of Animal Behavior

Cloudsley-Thompson (1961a) has cautioned the student of animal behavior on the errors of teleology and anthropomorphism. The former pitfall, present in all investigative work, involves purposive explanations, where a result is treated as a cause (Miller and Haub, 1956). Anthropomorphism - the ascription of human characteristics to things not human - is often more difficult to avoid. Moreover, there is not unanimity of opinion on the matter of anthropomorphism. Some recent views on this subject are of particular interest.

Carrighar (1965, pp. vii-viii) prefaces the text to her popular book on behavior with the following comments.

> The value of understanding our behavioral roots is slowly becoming recognized, and yet ethologists are still, sometimes, accused of anthropomorphism. The charge is not really logical. For many decades it has been known that those high forms of animal life, the vertebrates, are related in such anatomical structures as skeletons. The wings of birds, the forelimbs of bats, horses, whales and men are all, of course, built on the same general plan, as no one now denies. More recently glands have been seen as related in many species. The hormones secreted by ductless glands are so similar that those of one species are often injected therapeutically into a quite different species; when our own hormones are deficient, many human diseases are relieved or cured by hormones extracted from animals. Those hormones control much of the seemingly voluntary behavior of the animals - and of us - and yet the ban on anthropomorphism has prevented the recognition of likenesses between human activities and those of our subhuman forebears.

The above passage seems to me to be both accurate and timely. It should not, however, lead to the assumption that all behavior observed in other vertebrates has its closely related counterpart in human behavior, or vice versa.

Darling (1963, vii-viii), whose work during the 1930's on the behavior of red deer is a pioneering classic, comments as follows on the philosophy of sea level, and a range of altitude from 1560 feet at Lake Beldon to 2693 feet at the summit of Goodnow Mt. Other than swamps and meadows relatively level areas are exceptional.

The rectilinear drainage system (Balk, '32) on the Forest, including eleven named bodies of water and numerous streams, drains through Rich Lake to the Hudson River. The gradient of all streams about 1700 feet is quite steep, most of them flowing over rocky irregular beds. Below 1700 feet, as shown by the drainage from Catlin Lake to Rich Lake, the streams flow sluggishly through numerous swampy areas and broad valleys.

Figure 1 shows the location of the major lakes, streams, and mountains of the Forest.

Geology and Soils

Isachsen (1962) has presented a brief but valuable geological history of the Adirondacks. He states that the ancestral mountains, "...perhaps as magnificent as the Himalayas.", were formed approximately 1100 million years ago. Since that time they have had a varied and complex history, with glaciation playing a major role in relatively recent times. Probably most signficant from the biological standpoint, was the removal of residual Tertiary soils, and the formation of numerous lakes and ponds.

Smith (1955) states that the underlying rock of the region is nearly all igneous or metamorphic, and has produced a thin, infertile, sandy soil generally classed as Gloucester. Heady (1940) characterizes the soils of the Forest as podzols for the most part, largely of the three types of mor humus recognized by Heiberg (1937).

Detailed accounts of the geology of the Forest may be found in Heady (1940) and Black (1943).

Climate

As detailed accounts of the local climate will be presented in subsequent chapters, the following comments are both brief and general.

Smith (1955, p. 129) summarizes the climate of the Adirondack Division as follows:

> The region has a mean annual temperature under 45°F., with a January and February mean of under 20°F. The average annual minimum temperature is -25°F. In July the mean temperature is between 60° and 68°F., and the growing season is between 90 and 130 days with that for most of the area being under 120 days.

> Precipitation ranges from 60 inches annually on the western slopes exposed to the storms off Lake Ontario to 30 inches on the lee side of the mountain mass. The annual snowfall averages 80 inches or more, and is particularly heavy in parts of Herkimer and Lewis counties where it is over 180 inches in some localities.

Mordoff (1949) places the Adirondacks in the Northern Plateau climatic division. He gives the average length of the growing season as 105 days, and the mean temperature as under 60°F. The mean annual precipitation is 40 to 50 inches distributed evenly over the year, and the mean annual snowfall is 80 to 100 inches. The mean minimum temperature for January is between 5° and 10°F., and the mean maximum for July less than 80°F. Percent of possible sunshine ranges from between 35 to 40 percent in January to about 60 percent in July. The mean annual relative humidity at 7:30 A.M. exceeds 80 percent.

Thus, the regional climate may be characterized as cool and moist, with cloudy weather predominating. Growing seasons are relatively short, winters relatively long.

The climate of the Huntington Forest as summarized by King, et al. (1941), and Patric (1958), is very similar to that of the region. January is generally the coldest month, July the warmest. Prevailing winds are from the west and north. Cloudy days outnumber clear and partly cloudy days which occur in about equal numbers. The growing season averages about 122 days (Patric, 1958), somewhat longer than the regional average of 105 days given by Mordoff (1949).

Vegetation

While the flora of the Adirondacks is relatively simple in composition, it varies greatly from one section to another, and broad classifications are difficult to make realistically. Dice (1952) indicates that Shelford includes both the Deciduous and Coniferous Forest biomes in the Adirondacks, and according to Merriam the region is in the Transition zone occurring between the Upper Austral and Canadian life zones. Dice himself places the region in the Canadian biotic province.

Because detailed ecological classifications have little relationship to this study, I have chosen to utilize what are commonly called forest cover types for the bulk of the work. These types simply describe present conditions, and appear to be adequate for relating to deer behavior. As background, Smith's (1955, p. 129) comments on the forests of the region are pertinent. (The scientific names of all plants mentioned in thetext are listed in Table 30, Appendix I).

> In general, the area below 1500 feet is occupied by a northern hardwood forest of beech, yellow birch, sugar maple, hemlock, and paper birch, with an admixture of balsam fir and red spruce. The heart of the area is predominantly spruce, fir, and birch, becoming a stunted forest of spruce, fir, and paper birch on the exposed summits.

While the Huntington Forest is in the heart of the Adirondacks, its forests contain less of the coniferous components than is indicated above. This is probably the result of heavy cuttings for softwood pulpwood and timber which preceded the 1930's (see next paragraph). Generally, the forests here may be characterized as follows:

Upper elevations - largely coniferous, mostly red spruce;

Middle elevations - mostly hardwood, beech and sugar maple predominating, with some yellow birch and conifers;

Lower slopes and drier bottoms - predominantly mixed-growth with hemlock, red spruce, and yellow birch comprising the bulk of the stands; and,

Bottoms, swamps, lakeshores - mostly coniferous, varying with site from spruce-fir to white cedar.

The relative abundance and distribution of these types is shown in Figure 2(not included in the printed copies).

The logging history of the Forest helps to explain present conditions, and is pertinent to problems dealing with deer ecology and behavior. The following brief account is based upon unpublished reports and personal communications furnished by Messr's. E. F. Patric and W. C. Tierson.

During the late 1800's most of the Forest was logged for softwood, principally white pine and red spruce. Another softwood cutting was made in the southeastern part of the Forest in 1928. Little cutting was done from then until 1943, but the large commercial clear-cut initiated in 1943 took both softwoods and hardwoods. After an interruption of several years, the cutting began again in 1946, and was completed in 1949. Since then, smaller cuttings have been made almost annually, principally for hardwoods.

The cuttings prior to the 1940's must have changed the composition of many stands. The removal of softwoods from mixed-growth stands tended to result in their resembling hardwood forests, and in softwood stands where abvance reproduction was not abundant, the resulting forest probably resembles mixed-growth. The important point is that softwood acreage and volumes were decreased, while hardwoods increased. More recent cuttings tend to have the opposite effect, with softwoods increasing at the expense of the hardwoods. This picture is complicated considerably by the feeding habits of the deer, but they too, generally tend to favor an increase in softwood, with the notable exceptions of hemlock and white cedar.

Lesser vegetation is prominent over much of the property. Shrubs are present in both the forest understory and openings, with witch-hobble prevailing under many overstories, and red raspberry dominating most openings immediately after logging. Alders and willows are common in wetter sections. Both witch-hobble and raspberry are important items in the diet of the deer.

Grasses and sedges are common in the few meadows and marshes of the Forest, but sparse in the forest proper where herbs predominate. Both emergent and floating-leaved aquatic vegetation is abundant in some sections, and, in particular locations, is utilized heavily by deer.

Animal Life

According to Allee et al. (1949), the Taiga biome is characterized by furbearers of the Mustelidae, rodents, and lagamorphs, while the most conspicuous larger mammal is the moose (Alces alces). The Deciduous Forest biome, on the other hand, is characterized by the white-tailed deer, the black bear (Ursus americanus), the opossum (Didelphis virginiana), the raccoon (Procyon lotor), and numerous rodents and insectivores. Smith (1955) lists the white-tailed deer, black bear, and the varying hare (Lepus americanus) as important game mammals of the Adirondack region. Vertebrates of the Forest have been listed by Johnson (1937) and King, et al. (1941). From these and current observations it is clear that the mammalian fauna, like the flora, represents a transition between zones. Currently, the white-tailed deer and the black bear are the only large mammals present, but several species of mustelid furbearers occur. The raccoon is common but not abundant, and the varying hare is the only lagamorph present. Rodents are numerous in the form of many small mammals, and at least two genera of shrews occur here.

Thus, the larger mammals are those of the Deciduous Forest biome, the medium-sized forms more representative of the Taiga, and the smaller mammals characteristic of both.

In addition to mammals, all other classes of vertebrates excepting the Cyclostomata are present on the Forest. Fishes and amphibians are numerous and abundant, but reptiles are few, being represented largely by but one species of snake, and one turtle. Birds are abundance, particularly during the spring and summer months.

Species which may affect deer ecology and behavior include both predators and parasites, and "competing" herbivores. Predators present which may affect deer are the bobcat (Lynx rufus), coyote (Canis latrans), red fox (Vulpes fulva), and the fisher (Martes pennanti) (Pringle, 1964). Predation by the fox and the fisher is likely restricted to young fawns. Parasites of deer are numerous in this region, but related to this study only two groups of biting flies are probably important - the deer flies (Tabanidae) and the blackflies (Simulidae). While relatively little is known of the competing aspects of other herbivores, it is doubtful if they seriously affect deer behavior, with the possible exception of the activities of the beaver, which may influence deer distribution through their cutting, damming, and flooding.

The Deer Population

A history of the Adirondack deer herd has been presented by Severinghaus and Brown (1956). As the Huntington herd has long been unhunted, except by limited poaching, detailed information on the population is lacking. The following brief account does, however, provide some background.

Deer were apparently not abundant enough here prior to 1900 to materially suppress hemlock reproduction, a favored browse species in this area. A sample of 99 small-sized trees (10 inch d.b.h. maximum) showed that 94 percent were 60 or more years old. Fifty percent were found to be between 61 and 80 years old, while but 6 percent were less than 60 years old. By deduction, I conclude that a sharp increase in deer density occurred here about 60 years ago. Quantitative information on deer densities was first obtained in 1939 when drives indicated one deer to 15.4 acres (Webb, 1948). Smaller drives in 1946-47 showed one deer to 25 acres (Steinhoff, 1947). Pellet group counts in the 1950's and track counts in the early 1960's indicated a population averaging one to 45 acres (Huntington Forest,unpub. data).

From this account it is tempting to conclude that deer numbers increased sharply just after the turn of the century, and continued to increase until sometime in the 1920-30 period, after which they declined until the 1950's when they stabilized. While this general trend may be accurate, the magnitude of the decrease was probably less than the figures indicate, as different methods, some of which involved considerable error, were employed in the estimates.

The factors that actually limit the population are not known. Decimating factors include illegal kill, winter mortality, predation, and road kills. Some emigration occurs, and may, combined with a complex of decimating factors, serve to effectively limit the population.

Little is know of the age and sex structure of the herd, or of its rate of productivity. Crude field observations indicate that the sex ratio approaches equality, and that realized productivity is about 1.2 fawns per doe (yearlings and older).

Collection of Data

Indirect Measures of Deer Activity and Distribution

Road Track Counts. - Track counts have often been employed in attempts to census deer (Steinhoff, 1947; Wright, 1954; Tyson, 1959). In this study track counts were employed to provide the bulk of data on deer distribution, and to furnish an estimate of activity. Counts were always made for a known period of track accumulation, usually four, 12, or 24 hours. Tracks existing prior to the period of accumulation were either obliterated or tallied before the period began. Depending on the season, and condition of the road, obliteration was accomplished by raking with a standard road rake, dragging brush, or, when snow prevailed and tracks were relatively sparse, running over the deer tracks with the track of a snow-mobile. Counts were made from various vehicles; in the spring, summer, fall, and early winter periods from a cab-forward jeep or a bicycle; in mid and late winter from tracked vehicles. The usual track count was a 10.5 mile loop, or sample sections thereof (Figure 1). Counts were planned weekly, and were executed as permitted by weather and road conditions, and availability of operational vehicles. Counts were made from the summer of 1963 through the winter of 1965-66.

The major unit of measure employed was the presence or absence of tracks in permanently-marked five-chain sections of road. Other scoring systems were tried in an attempt to record more detail, such as the probable number of deer, and their general direction of travel. While these measures occasionally provided valuable data, often the track picture was too confused to be recorded accurately, except for the presence or absence of tracks.

Track and Bed Counts in Wintering Areas. - Most of these counts were made in the Deer Creek concentration area (Figure 1). A two-mile route with permanently-marked stations located every chain was followed, and the locations and numbers of tracks, trails, and beds were tallied. Individual bed sites were marked with coded plastic flagging so that reuse patterns might be ascertained. This work, planned for the winters of 1963-64 and 1964-65, was conducted largely during the former period, as shallow, heavily crusted snow in the latter winter resulted in sparse concentrations of deer, and difficult recording conditions.

Direct Measures of Deer Activity and Distribution

Extensive Roadside Counts. - Records of deer seen along the Forest road system were made by many individuals from the summer of 1963 through the winter of 1965-66. Observation forms were carried in all work vehicles, and in many private automobiles. Date, time, and location to the nearest chain were recorded for each sighting. When discernible, additional observations were made of marks, sex, age, and behavior.

Intensive Observations. - The following methods were employed for more intensive observation of deer.

Lakeshore Counts: Most of this work was done during mid-day hours in the summers of 1964 and 1965. Periodic counts of deer seen were made, as were accounts of feeding and social behavior. This work was done at Deer Lake (Figure 1).

Spotlighting Counts: These counts were conducted during the spring and summer of 1964 and 1965, with many more observations made in 1965 than in 1964. In 1965 the counts were made over a route about three-and-three-quarter miles long, with deer sighted on both the out-going and in-coming legs of the trip being recorded. All of the counts were made between 11:00 P.M. and 1:00 A.M. (EDST).

Observations at Mineral Licks, Feeding Stations, and Meadows: These observations were made irregularly from 1963 through 1965. Principal objectives of this work were to observe marked deer, social behavior, feeding behavior, and bedding. The mineral licks, while not natural, were not established for this study, but are the result of stockpiling salt and sand for winter road maintenance (Figure 1).

Marking of Deer: From 1961 through 1965 deer were captured, marked, and released for subsequent observation. Most of these deer were captured during the summer of 1964 as a part of this study. Newborn fawns were captured by hand, and marked either with metal or plastic ear tags, or both. Other animals were captured by immobilization with drugs, mostly nicotine alkaloid, which were carried by projectile syringe delivered by a gas-powered rifle (standard equipment of the Palmer Chemical and Equipment Company, Inc., Douglasville, Ga.). The technique as employed here was described by Behrend (1965). Captured deer were marked with various combinations of metal ear tags, plastic ear streamers, and plastic collars.

Measurement of Weather

Base Station. - The Forest base weather station, a cooperative station of the United States Weather Bureau (Newcomb 4WNW), has been in operation since 1938.

Temperature, relative humidity, precipitation, snowfall, snow depth, and barometric pressure have been recorded for most of this time. Wind velocity has been recorded continuously since the early autumn of 1964. The station is located near the south end of Arbutus Lake (Figure 1).

Temperature, relative humidity, and precipitation are recorded on seven-day charts by a standard hygro-thermograph, and a weighing type rain gauge (Belford Co., Baltimore, Md.). Atmospheric pressure is recorded on a seven-day barograph (Taylor Instruments Co., Rochester, N.Y.), and wind is recorded by an Esterline-Angus, 0-1 millampere recorder, fed by a Hydro Products Co. anemometer (San Diego, Calif.). Snowfall and snow depth are measured once daily.

Wintering Area Stations. - Five weather stations were operated in the Deer Creek winter concentration area during the winter of 1964-65, and four during the winter of 1965-66 (Figure 1). Hygro-thermographs recorded temperature and relative humidity, and totalizing anemometers measured miles of wind. Four stations were located in the forest, one in each major forest type, while a fifth was located on an exposed lakeshore. Snow depth was measured at selected locations during the winter of 1963-64, and at randomly selected locations thereafter.

Other Stations. - Additional weather recording stations were located in areas of particular interest, e.g., lakeshores, openings, etc., where they were operated for parts of the summer.

Measurement of Vegetation

Food. - Relatively little quantitative work on deer-food relationships was included in this study. That which was done was simply an attempt to provide insight into some rather obscure relationships which could affect deer distribution and activity.

Samples of water shield, a floating-leaved plant resembling a small, delicate pond lily, were taken in Deer Lake to document its density at the beginning and near the end of the summer of 1964. Six beds of vegetation were delineated on an aerial photograph, and sampled by counting the number of floating leaves contained by a plastic hoop thrown in a random fashion from a canoe. Ten samples were taken in each bed.

Two hardwood browse species, sugar maple and striped maple, were sampled to document changes in "hardness" during the late summer and early fall of 1964. Approximately 100 twigs of each species were sampled periodically during August and September, with peelability of bark of the current year's growth used as the major unit of measure.

A crude comparison of abundance of browse on the periphery and in the center of the Deer Creek winter concentration area was attempted in the fall of 1964. Ten plots were randomly located in each area, and the number of browsable twigs recorded by species. Due to the large variation present, the sample proved to be inadequate for statistical analysis, but provided interesting descriptive information.

Cover. - Coniferous crown cover and basal area were estimated at 167 points in the Deer Creek concentration area. Crown cover was estimated by the spherical densiometer technique (Lemmon, 1957), basal area with a 10-factor wedge prism. Changes in cover in a hardwood stand were documented by periodic sampling during the fall of 1964. Crown cover and low-level cover (3 feet) were estimated at 54 points, the former by the densiometer technique, the latter by use of a modified target-type density board described by Wight (1938).

Classification of Types. - The Deer Creek concentration area was typed by field reconnaissance and interpretation of aerial photographs. Types were derived from those listed by the Society of American Foresters (1954). Each five-chain section of road on the principal track count route was typed in a similar manner.

Documentation of Physiography

Aspect was recorded for all five-chain sections of road over the track count route, and for the 167 stations in the winter concentration study area. Presence or absence of streams or lakeshores was also recorded over the track count route.

Analysis of Data

Tabular and Graphical Analysis

Data from track counts, deer counts, weather stations, etc., were summarized and graphed as accumulated for the detection of trends. Because of the nature of some data no statistical analysis was attempted, and interpretation of the graphs was the final analysis.

Statistical Analysis

Simple correlation statistics were used to examine the relationship of deer activity to individual environmental variables. Multiple and partial correlation techniques were employed to evaluate the relative roles of various weather factors and season in influencing deer activity. An I.B.M. 1620 computer was used for the multiple analyses.

Variations of Student's t-test were used to compare means where but two cases were involved, and where three or more means were involved the analysis of variance was employed. Confidence intervals for means were used frequently as the best descriptive statistic available.

Variations of the chi-square test were used to analyze logically discrete data, and to examine goodness of fit and independence of certain observations.

Results of the tests of hypotheses are indicated as significant at probabilities of .01 and .05. The *apriori* level of significance selected and employed throughout the analysis in all of the tests of significance was .05.

Intuitive Analysis and Deduction

Intuitive analysis was employed where grossly inadequate or subjective data alone were available. Deductive reasoning was used to reach conclusions, and to examine their validity.

Some Problems and Limitations

Problems of logistics, scheduling, and weather often made it impossible to obtain sufficient amounts of data, or to maintain the desired continuity of sampling. Problems in statistical design and analysis were also numerous.

So relatively little is known of the quantitative aspects of deer behavior, that what constitutes adequate data can hardly be determined apriori. Moreover, practically nothing is known of the mathematical distributions which underlie most of the observations made in this study. Both of these problems thus deserve study in their own right. Also, most of the observations of deer behavior were not made in a random manner,either in time or space, and true replication in space was never attained. In the strictest sense therefore, statistical inference is limited to the population under study alone.

One of the most difficult statistical problems encountered in this work was that of lack of independence of observations. One example of this is the contiguous five-chain sections of road used to record tracks. Here, the probability of a given section containing a track was clearly greater for a section adjacent to another section with tracks, than it was for a section adjacent to sections without tracks. This largely restricted analyses of activity for a given count to comparisons of large, separate sections of road, on the basis of totals, percentages, and proportions only.

These problems are mentioned here so that they need not be continually pointed out in the following chapters, and to better prepare the reader to evaluate the results. Accordingly, these problems should be at least generally understood, and kept in mind throughout the results and conclusions sections.

CHAPTER III

LIFE HISTORY

Much has been written of the life history of the white-tailed deer, and many of its general habits are widely known. Thus, the summary presented here is brief, and intended only to cover the most important points in order to provide a sound basis for the understanding of subsequent chapters. For a comprehensive treatment of the subject, the excellent work of Severinghaus and Cheatum (1956) should be consulted.

Deer breed in autumn in the Adirondack region, largely between mid-October and mid-December, with a peak in breeding activity in mid-November. During this period, commonly known as the rut, mature males actively pursue breeding females, and are intolerant of other breeding males. The female's estrus, or heat period, lasts about 24 hours, and reoccurs in approximately four weeks if fertilization does not take place. Conception is followed by a gestation period which averages about 200 days (Severinghaus and Cheatum, 1956). During the rut deer are usually widely distributed, and are found in many vegetation types.

Breeding activity decreases with the coming of winter, and the males shed their antlers in December and January. As snow cover deepens, open areas and hardwood forests are used less, and deer are found in increasing numbers in coniferous and mixed-growth stands. Maintenance of snow cover deep enough to affect travel results in concentrations of deer in the coniferous areas, where the snow is shallower, and travel easier. These areas also provide some protection from winter winds, which, in concert with cold, may produce discomfort and stress.

The concentrations of deer in the wintering areas, and in areas of abundant food at other seasons, are aggregations of animals formed by environmental influences, and are not social groups. These aggregations are, however, comprised of both small social groups, and individuals. During the period of winter concentration, large numbers of deer exist on far less area than during other seasons, and, with part of the potential food supply covered with snow, it is often a time of semi-starvation.

As snow depths recede in the late winter and early spring, concentrations break-up and distribution widens. Observations of marked deer on the Forest indicate that many deer are on their summer-fall ranges in April and May. Actually, during mild winters at least, most deer probably winter on a restricted portion of the range they occupy during the rest of the year. Moulting of the heavy winter coat usually begins in April, and is completed by mid-June when most animals are in their thin, red summer coats. The antlers of the males begin to grow in the spring, and continue to grow throughout the summer.

Fawning generally begins after mid-May, but most fawns are born in June. On the Forest most does bear a single fawn, but twins are not uncommon. Development of the young is rapid, and most fawns lose their spotted-coats in September when they begin to assume the heavy, gray coat of winter. Adult deer begin the process in late August and September, and are usually fully clad for winter by mid-October when the rut begins. By this time the "velvet" has been shed from the buck's antlers, and the rubbing of small samplings begins in earnest.

In many parts of the range of the white-tail, functional sexual maturity is attained by females during their first year, but here does first breed as yearlings, not as fawns. While recent evidence (Silver, 1965 a, b) indicates that male fawns in captivity can successfully breed, it is generally held that males ordinarily mature as yearlings (Cheatum and Morton, 1942). Full development in length, height and weight is attained from four-and-one-half to five-and-one-half years of age (Severinghaus and Cheatum, 1956).

The white-tail, like all Cervids, is a ruminant, or cudchewing animal, and possesses a complicated but effective digestive system. It is almost exclusively herbivorous, and capable of utilizing woody growth (browse) for food. During the summer and fall many kinds of plants are eaten, but in winter browse is the staple food. Being completely dependent on plant food, deer are generally quite responsive to changes in quantity and availability of vegetation. Because of its particular feeding habits, the deer usually has a substantial effect on its own environment, often changing the species composition of forests, reducing its own food supply, and producing changes in coniferous cover.

Many of the important details of the deer's life history will be discussed in the following sections and need not be mentioned here. So that the following pages may be entered with the greatest facility, I offer the following summary of the most important points of the life history of the white-tail.

Foremost is the fact that the deer is a herbivore, and is generally responsive to changes in the plant food supply. These changes, and seasonal climatic changes that affect mobility, both may result in aggregations of animals in restricted areas. Social groups within the aggregations are relatively small, the single family unit, i.e., doe and immature young being the basic group. The annual reproductive cycle, including changes in the secondary sex characteristics of the males, is relatively long and complex, and evokes difference behavior at different stages. Finally, the summer and winter coats of the deer are strikingly different, and climatic factors may consequently affect behavior differently at different seasons.

For the most thorough understanding of the results which follow, these points should be understood, and kept constantly in mind.

CHAPTER IV

DISTRIBUTION

Review Of The Literature

Nearly everyone who has written on the ecology or natural history of deer has stated where they are found at different times of the year. Consequently, the body of literature dealing with seasonal distribution is immense, and only selected works can be reviewed here. Before dealing specifically with where deer are found at different times, I have chosen to review the general nature of changes in distribution, how these changes may be effected (movements), and why deer change their ranges seasonally.

Seasonal Distribution

In northern and mountainous regions deer generally occupy different ranges in winter than during other seasons; or, perhaps stated more precisely, different parts of the annual range are occupied at different seasons. In the Adirondacks, Severinghaus and Cheatum (1956) state that only 12 to 13 percent of the fall range is usable in winter. They cite other reports which indicate that on other northern ranges from seven to 10 percent of the total range is used in winter. In the mountains of North Carolina, the winter range has been estimated to be about one-third of that of summer (Schwan and Swift, 1941). In Missouri, Progulske and Baskett (1958) concluded that the amount of movement by white-tails during all seasons more closely resembled that of Texas, than that of more northern ranges. In Texas, seasonal movements are very limited (Hahn and Taylor, 1950), and deer do not move great distances in search of food even during periods of shortage (Hahn, 1945). In the mountains of Arizona, Welch (1960, original not seen) found seasonal movements restricted to local changes in distribution regarding exposure and cover only.

The magnitude and nature of seasonal movements which result in changes in distribution have long fascinated students of both white-tailed and mule deer (O. hemionus). Movements are usually more pronounced in mule deer than in white-tails, but as Siglin (1965) points out, this is probably due more to differences in habitats, than to inherent differences in the species. In both species the most extensive movements occur where seasonal climatic changes are pronounced, due either to high elevation or northern latitude (Severinghaus and Cheatum, 1956; Siglin, 1965). Siglin presents an excellent review of the movements of mule deer, and only those of white-tails are treated here.

The greatest amount of information on movements in white-tailed deer is from the Lake States. Severinghaus and Cheatum (1956) also credit this region with the longest migration of white-tails ever recorded, some 50 to 75 miles. This movement no longer occurs, having ended about 1870. Several studies in the Lake States have utilized deer that were trapped and marked on their wintering areas, and recovered on the fall ranges by hunters. In Wisconsin, Dahlberg and Guettinger (1956) found deer averaging 3.5 miles of movement, and Bartlett (1950) found most deer traveled less than 15 miles in Michigan. In Minnesota, Olson (1938) showed that males averaged five miles, and females less than one mile of movement. Hunt and Mangus (1954) recovered 70 percent of their marked animals within the "immediate vicinity" of the trapping area. Carlson and Formes (1957) found that movement by bucks averaged 6.7 miles, does 3.7 miles. Erickson, et al. (1961) recorded movements of deer in three different regions of Minnesota, and found that the average movements of males varied from 6.7 miles in the northern coniferous region to 14.0 miles in the prairie-deciduous regions, while movements of females ranged from 3.7 miles in the northern coniferous region to 9.0 miles in the deciduous-coniferous region.

Severinghaus and Cheatum (1956) cite examples of herd movements of 10 to 20 miles in the mountains of Wyoming and Montana.

In southern New Jersey, Wright (1954), found that most travel by deer did not exceed one mile, and Progulske and Baskett (1958) found that the average maximum distance moved in all seasons by deer in Missouri was 1.7 miles. Tyson (1959) found that deer in Florida usually ranged over an area less than a mile in diameter, and even less movement has been observed in Texas white-tails (Hahn and Taylor, 1950). Thomas, et al. (1964) found the average movement of marked deer in that region to be 717 yards from the point of marking, and they stressed the fact that all studies of marked deer in Texas have indicated very limited home ranges.

Home range itself serves well to illustrate movements and distribution. Where deer migrate, their annual home ranges must be considerably larger than where they do not move great distances between seasons. To my knowledge no quantitative information is available on the annual home range of deer that move from one seasonal range to another.

Several estimates of seasonal home range are available, however. Tyson (1959) found deer in Florida ranging over an area about two miles in diameter in late spring, but less than one mile in diameter in July. Hahn (1945) states that in the Edwards Plateau region of Texas, where annual and seasonal home ranges are identical, that home range rarely exceeds one-and-one-half square miles. Later results with belled deer (Hahn and Taylor, 1950) indicated that most deer on one study area remained with a 640-acre tract, while nearly 85 percent on another study area stayed within a one-mile radius. The recent results of Michael (1965) in Texas indicate annual home ranges of less than 430 acres for most bucks, and less than 150 acres for most does. He found that some deer ranged over more ground in winter, others more in summer. In Missouri, Progulske and Baskett (1958) found annual ranges for males to average 940 acres, and 400 acres for females. Respective summer ranges were 630 and 170 acres. In the spring, summer, and early fall, the animals most frequently observed ranged over about one-half square miles. Schoonmaker (1938) stated that under normal conditions, the home range of the deer in New York does not exceed one-half square mile, but may be larger during the rut, or when wounded and pursued. Severinghaus and Tanck (1950) tracked two wounded deer and found that one circled in an area of about 130 acres during a six-hour period, while the other coursed over about 1300 acres during two-and-one-half days. Severinghaus and Cheatum (1956) indicated that stained pellets from deer fed dyed feed were seldom found more than one-half mile from the feeding station. In Minnesota, Tester, et al. (1964) found that a doe being tracked by telemetry moved over an area slightly smaller than one square mile during 10-day periods in December and February. Again via telemetry, Tester and Heegan (1965) found that two does ranged over an area about one mile by three-tenths of a mile in January. During this period their largest daily ranges were four-tenths and three-tenths of a square mile.

Thus, it is obvious that considerable variation in seasonal movements, home range, and changes in distribution occur over the range of the white-tail. Even within one state, e.g., Minnesota, where essentially the same method has been employed in several studies, results on movement vary. I believe that the main reasons for these differences are differences in habitat and climate, both current and past, which have produced different patterns. One generalization appears possible however: deer tend to move farther and/or distribute themselves in much different habitats where changes in climatic conditions are more pronounced, and move little, or not at all, where the climate is milder and more stable.

What really causes seasonal movements of deer? Presently, there is considerable information on factors which correlate with changes in distribution, but little on what actually causes them. Moreover, there is not complete agreement on how some factors which correlate with movements act upon the animals.

Severinghaus and Cheatum (1956, p.158) summarize their views on this problem as follows:

> The immediate initiating factor that prompts migration is difficult to determine, for the more obvious climatic factors and the pattern of quality and availability of food differ widely in the whitetail range. The fall or early winter migrations appear largely to be responses to weather conditions which affect the animals' physical comfort; at these times they seek areas which provide adequate shelter from harsh winter conditions. The spring movement back to summer range appears to be a release from a restricted food supply

> during which the animals move out to the newly available spring forage.

They go on to say that in winters with little snow, and moderate temperatures, deer will generally stay on their summer-fall range.

Shiras (1935) is quoted by Siglin (1965) in describing the now extinct 50 to 75 mile migration from Michigan to Wisconsin: "Sometimes as early as August 15, on the coming of the first heavy north winds and light frosts, the does, fawns, and yearlings started south and by September thousands were on their way...". Hammerstrom and Blake (1939) found that a weekly average temperature of about 20°F. appeared to initiate both winter concentration and spring dispersal in Wisconsin.

Snow is generally conceded to be the most potent factor affecting seasonal movements and distribution of deer. Formozov (1964) has presented a comprehensive review of the relationship of snow cover to the movements and distribution of cervids in Europe and Asia. Day (1963) has surveyed the literature for white-tailed deer, and found most authors considering snow the foremost factor influencing distribution. Kabat, et al. (1953) have cited a depth of 18 inches as that which initiated dispersal in the spring, and Telfar (1965) found that depth of 14 inches iniatiated movements toward wintering areas in the winter, and away from them in the spring. Banasiak (1961), however, dissents, citing that many times "yarding" begins before traveling is hindered. He concludes that deer seek places offering them the greatest physical comfort rather than any other benefit.

Studies of other species of deer may be briefly reviewed for a broader perspective. Both Russell (1932) and Dickson (1934) found that snow initiated the downward movement of mule deer in the fall, but disagreed as to the cause. Russell believed that the movement was solely in response to a reduction in the availability of food, and Dickson that the cause was anticipation of increased vulnerability to predation that comes with deep snow. McCullough (1964),however, found that neither snow nor reduced food supplies affected movement of black-tailed deer (O. h. columbianus), but that both the spring and fall migrations occurred when the minimum relative humidity for a period was between 40 and 60 percent. Darling (1937) found that concerted movement of red deer in Scotland preceded falls of snow by two days, and cited instances of movement of deer on the European continent several days in advance of snowstorms. He summed up by saying (p. 137): "We see, then, that snow in its onset and disappearance leads to the most spectacular movements of the deer, and there are secrets remaining for us to learn of the animals foreknowledge." Bergerund (1963) illustrates the tremendous influence of snow on distribution of a caribou (Rangifer tarandus) population which ranged over 16,000 square miles with five inches of snow on the ground, but was compressed into an area of 3,600 square miles when snow depths were from two to four feet.

As Siglin (1965) points out, spring movements of both white-tailed and mule deer occur principally in response to the development of spring vegetation. This apparently holds for elk (Cervus canadensis) also.

Relatively little is known of the mechanics of how deer choose travel routes and wintering and summering areas, and how winter aggregations are formed. The most definitive information available is from recent studies of mule deer which indicate that deer wintering together do not all summer together, and vice versa (Ashcraft, 1961; Gruell and Papaz, 1963; Zalunardo, 1965). Gruell and Papaz found that fawns and yearlings both accompanied their dams in traveling to their wintering areas, and, upon reaching maturity, retained the pattern all their lives. Zalunardo believes that yearlings probably disperse on the summer range but return to the wintering grounds to which they first traveled as fawns. Whether or not these basic patterns prevail in white-tails must be answered by future work, but Progulske and Baskett (1958) cast doubt on the problem by citing some evidence that deer in Missouri may not return to the same seasonal ranges year after year.

Habitat Preferences

As winter has been long-considered the critical season for deer, most of the literature dealing with habitat preferences concerns the winter range. The following review includes distribution on both ranges, with emphasis on the habitat of deer in norther regions.

Winter Distribution. - In the central Adirondacks, Severinghaus and Cheatum (1956) state that wintering areas are largely restricted to spruce slopes at lower levels, and to coniferous swamps. Webb (1948) studied winter range on the Huntington Forest, and found that concentration areas were not related to elevation, but that they tended to be either on level land or the steepest slopes. North-facing slopes were avoided despite their abundance of food, and concentration areas tended to be the densest coniferous areas which were often deficient in food. Krull (1964) studied winter deer use of two areas on the Huntington Forest, and concluded that only during the severest mid-winter weather did the animals use an uncut shelter area more than a clear-cut area where food was plentiful. Spiker (1933) points out that during mild winters, Adirondack deer may be found on their summer range for a large part of the season.

In central New York, Cook and Hamilton (1942) found that deer congregated on favorable south and southeast slopes that were protected from the wind, and where exposure to the sun kept snow at minimum depths. Severinghaus and Cheatum (1956) cite reports of Seamans which indicate that Vermont deer winter in protected valleys, with southern or southeastern exposures, which protect them from the prevailing winds.

In northern Maine, Banasiak (1961) states that deer concentrate in fairly mature stands of conifers, working out into hardwood and mixed-growth stands for food; while deer in southern Maine roam over much of their summer and fall range except during cold, windy, or stormy weather when they seek coniferous shelter. Day (1963), and Gill (1964), indicate that white-tails in northern Maine strongly prefer spruce-fir forests for bedding, and Telfar (1965) reports that deer in Nova Scotia winter in this same type.

Wintering areas in the Lake States appear to vary widely from place to place. In Michigan, either coniferous swamps or mixed coniferous and hardwood stands are used (Bartlett, 1950). In Wisconsin, however, Swift (1946) found that deer will "yard" in both coniferous and hardwood areas, and in uplands as well as lowlands. Tester and Heegan (1965) found that white-tails in Minnesota in January concentrated in a cedar bog during cold weather, but ranged several miles into the adjacent uplands during warm periods.

In areas with less severe winters, such as southeastern Ohio, winter use of coniferous shelter is very limited, and deer are found in a variety of cover types during all seasons (Chapman, 1939). In Missouri, Progulske and Baskett (1958) found that individual deer ranged over larger areas in winter than in summer. As mentioned earlier, white-tails in the southern United States occupy essentially the same range year-around.

Recent studies in Maine have provided interesting information on preferences of deer for winter bedding habitats. Day (1963) and Gill (1964) indicate that most sites are in densely-stocked stands of spruce-fir, and that beds are generally located within four to five feet of the base of a sizeable tree. Most beds are found at sites with at least 40 to 50 percent crown closure. Southerly aspects are generally favored, and some degree of preference was observed for sites on small rises, e.g., knolls and the edges of benches. Day found that the densest coniferous cover was used for bedding in extremely cold periods. Robinson (1960) studied captive deer in central Maine which were placed in pens with differing amounts of coniferous cover. He found that even with differences in the gross cover and climate in the different pens, the deer were so adept at choosing bed sites which provided protection from the wind and cold that no differences in condition of the test animals could be attributed to the differences in the cover.

des Meules (1964) believes that moose (Alces alces) in Quebec require a minimum of 20 to 24 inches of soft snow for bedding, the deep, soft snow serving as insulation to prevent chilling. Moose, accordingly, distribute themselves in cover providing a snow preferendum which lies between this depth, and the 40-odd inch depth which is the minimum tolerable for unimpeded movements. No such behavior has ever been suggested in white-tailed deer to my knowledge.

Before leaving the subject of winter distribution, some mention should be made of the minimum depth of snow that affects mobility in white-tails. Day (1963) found varying reports in the literature, with estimates ranging up to 24 inches. Hepburn (1959), who studied this phenomenon in Ontario, found that the steepest decline in mobility occurs between 10 and 16 inches, with thresholds of effect at 14, and nearly 20 inches. Deer, presumably, distribute themselves accordingly.

Webb (1948) concluded that cover is the factor which determines the areas in which deer concentrate in winter, and that areas containing the most food are not heavily utilized. Severinghaus and Cheatum (1956, p. 141) sum up their discussion of winter range by answering the question of why it is winter range, as follows: "Seemingly because shelter is better, it is warmer, less drafty, the snows not so deep, and, if the area is mountainous, it is generally found on the sunny side of the slopes." Townsend and Smith (1933, p. 213), who studied deer in all seasons in the Adirondacks, appear to be the sole dissenters on this basic point. They state: "As food is the main factor determining the activity of deer in summer so it is in winter. Without doubt food is, probably, a major factor in the selection of yarding grounds, although another important factor may be that of shelter."

Non-Winter Distribution. - Compared to winter distribution, relatively little has been written of the spring, summer, and fall haunts of deer. Severinghaus and Cheatum (1956) indicate that summer range, which they appear to use synonymously with non-winter range, may consist of almost all land area except for extreme elevations.

They state that this range is an area with good forage, and as the season progresses and foods change, local areas of abundant and depleted food are alternately occupied and abandoned.

Ruff (1938, original not seen) found that deer in mountainous North Carolina generally were evenly scattered throughout all types in summer, concentrating locally only to avoid excessive heat and flies. After many plants had hardeded in late summer, he found that deer frequented areas with early fruit, moving to mast-producing areas in the fall. In the hills of southeastern Ohio, Chapman (1939) recorded deer use of several types, or components of the habitat, and found that meadows were much-used throughout the year. Coppice growth was used highly during the spring, crops and orchards most in summer. Old hardwoods were used much in all seasons except summer, while scrub or second growth stands were used little except in winter. Salt licks were not highly used, but were visited far more in summer than in other seasons. In central Pennsylvania, Montgomery (1963) found deer spending the days in wooded areas, the nights in fields, and that they tended to bed during the night in fields near the lower limits of their ranges. Progulske and Duerre (1964) found that heavy night use of meadows in South Dakota by deer was closely related to availability of preferred foods, and that a combination of lush meadow growth interspersed with brush cover was most attractive.

In the Adirondacks, Merriam (1886) and Townsend and Smith (1933) found that deer were highly attracted to areas with aquatic foods during the summer. The latter found deer concentrated in areas of aquatic food in early and mid-summer, but rather evenly distributed throughout the woods in late summer. They believed that the distribution and activities of deer throughout all seasons was chiefly related to food.

Results

Seasonal Distribution - Patterns, Biotic And Physiographic Factors

Both track counts and observations of deer were recorded to attempt to document distribution over the year. Many of the results of these counts are summarized on the basis of the distribution of observations in four equal-length divisions of forest road (Figure 1). Some of the important characteristics of these divisions of road are listed in Table 1.

Track Counts. - The principal summary of the results of 75 track counts made over the entire ten-and-one-half mile route is shown in Table 2. These data clearly indicate that deer use of the four areas was relatively uniform from May through November, but quite different from December through April.

Observations of Deer. - A summary of over 2800 observations of deer made from the Forest roads is shown in Table 3. In marked contrast to the track count results, these observations are not uniformly distributed at any time of the year, and doubtless reflect more of the conditions for observation than the relative deer use of the different areas. For example, during the summer months from 200 to nearly 350 more observations per month were made in the Adjidaumo 0-205 division as in the Adjidaumo 210-Wolf Lake 135 division. As the track-count means (Table 2) for these divisions during the summer months are very similar, I believe that deer use of the areas was also similar, and that the differences in the magnitude of deer observations are largely attributable to the differences in cover conditions which influence the ability of observers to see deer. Thus, the division with large numbers of observations

(A 0-205) has open meadow associated with 48 percent of its route, while the lower division (A 210-WL 135) has no meadows, and is continuously forested (Table 1).

Accordingly, I conclude that over much of the Forest, direct observation of deer during daylight hours will not adequately document distribution. The details of these observations are presented here solely so that they may be compared to the track count results, and the unreliability of direct observations in forested areas made abundantly clear.

Direct observation of animals in restricted situations did provide consistent data. Counts made at Deer Lake during the day, and on the spotlighting route at night were useful in this respect. The results of these counts are presented in subsequent sections.

Distribution and Coniferous Shelter. - Deer use of four forest types with different amounts of coniferous overstory was examined, and the results may be summarized as follows: (1) no pronounced trends in either the type with scattered conifers, or the type with islands of conifers (these types approximate S.A.F. type 25, and transitions between 25 and 24[1] or 25 and 32 respectively); (2) the type with no conifers (type 25) used little in winter, with use increasing greatly from March to April; and (3) a definite trend in the type with continuous coniferous shelter (types 24[1] and 32) - high in winter, low in summer and fall; with a dramatic decrease from March to April followed by a regular decrease through August, followed in turn by a fairly regular increase from October through March (Figure 3).

On an areal basis the same late fall-early spring trend is shown by the Wolf Lake 140-Catlin Lake 210 division (Table 2). This division has 38 percent of its 5-chain sections in the continuous coniferous shelter type, while the other sections have five percent or less in this type.

Thus, in the winters studied, the overall trend toward heavy use of the coniferous shelter types appeared to begin in November and progress slowly throughout December and January, becoming generally established in February, and intensified in March. The trend reverses from March to April when distribution broadens rapidly.

It should be noted here that none of the winters included in this study was severe in respect to snow accumulation, and that the last two were particularly mild. Details of the character of these winters are given in the section on distribution and climatic factors.

Distribution and Other Aspects of Vegetation. - No relationship was detected between deer distribution and changes in either crown or low-level cover produced by the loss or gain of leaves by deciduous trees and shrubs. Similarly, distribution was not related to changes in the hardness of hardwood browse in late summer and early fall.

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[1] S.A.F. type 24 is not listed as occurring in this region, but this type best describes the many stands on the Forest.

According to track counts, sections associated with meadows were used about as expected on the basis of occurrence from May through October, and less during the remainder of the year. Sections with woods openings of various sizes were used only slightly more than expected, but consistently so from January through November.

Winter distribution was greatly influenced by logging which provided food in the form of tops from felled trees. Deer concentrated in these areas in winter and early spring. Similarly, spring and summer foods of particular attraction, especially aquatic food plants (see Chapter VI) concentrated deer in late spring and summer.

Distribution and Other Biotic Factors. - Some factors considered here were biting flies and human disturbance. No relationship of either to deer distribution was detected.

Distribution and Minerals. - In the spring and summer deer were abundant in areas of supposed mineral attraction where they were observed to eat soil and drink brackish water. This behavior generally begins in April, but is irregular until mid-May when deer are consistently seen in the areas of attraction. A summary of the distribution of observations of deer seen spotlighting in and around these areas is shown in Table 4.

During the latter part of May, about as many observations were made along the highway, which presumably provides early green forage and minerals, as were made around the salt lick alone. In June, however, the observations along the highway fall off rapidly and never recover, while observations at the salt lick rise through June and fall off but gradually through July. Apparently the green herbage along the highway is the major attractant here, and its attraction wanes rapidly in late spring. Minerals, however, appear to attract deer from late spring through July; and affect distribution by concentrating numbers of animals during this season.

Distribution and Aspect. - The distribution of deer use of five different aspects over the seasons was quite variable, but two points are worth noting. First, the south aspect was used consistently less than expected during all 12 months. More important, the west aspect (Figure 4) shows a fairly consistent trend with use rising from November through March, and falling off from March through November. During the entire period of December through March the west aspects were used more than expected.

Distribution and Shelter Type-Aspect Combinations. - The foregoing sections show that, considered independently, both shelter and aspect influence deer distribution, with shelter showing the more definite trends. Here, the relationship of the combined influence of shelter type and aspect are examined. A deer use index, completely analogous to those presented for type and aspect alone, but based on the December-March period rather than individual months, was calculated for the type-aspect combinations. These data are summarized in Table 5. The trend of major importance here is in the various combinations of shelter types with the west aspect. All of these show more winter use than expected on the basis of occurrence alone, and a progressive increase occurs from the no conifers type through the continuous conifers type.

Distribution and Other Physiographic Factors. - No relationship was observed between any other physiographic factors and deer distribution. Some of the factors considered were elevation, slope, and proximity to lake shores.

Seasonal Distribution And Climatic Factors

As indicated previously, deer are distributed quite uniformly over the Forest from May through November. Accordingly, the influence of weather on distribution must largely be restricted to the late fall to mid-spring period. However, as background for this section, and the subject of activity (Chapter V), the annual weather complex is reviewed briefly here.

Base Station Weather. - The weather record of the Forest base station (Newcomb 4WNW) is summarized in Tables 6 through 11. All of the measurements were made at heights slightly above that of a deer with the exception of wind which was measured at a height of about 30 feet in order to record general wind conditions rather than the extremely variable conditions near the ground.

The temperature statistics in Table 6 indicate that during the winter and spring when distribution is not uniform, the weather is considerably colder than during other months. For example, 0°F. or below temperatures occurred only in the December-April period. A more cumulative index is provided by degree days, where the totals are very much higher for the December through March period than during other months.

No striking patterns are shown by the relative humidity statistics shown in Table 7, but two points should be noted. First, saturation, i.e., 100 percent relative humidity occurs less frequently during winter than at other times. Next, the mean range (maximum minus minimum) is generally less in winter than in other seasons.

The monthly precipitation totals shown in Table 8 clearly show relatively uniform precipitation over the years of the study.

The accumulation of snow on the ground, however, is quite variable from year to year, and from month to month in the winter. A summary of snow depths during the December-April period over ten years is shown in Table 9. Here, the number of days with 10 or more, 15 or more, and 20 or more inches of snow on the ground is shown for each month for each year (these depths were selected after consideration of the results of Hepburn (1958) in his study of snow and deer mobility; see preceding literature review). The winters included in this study were slightly more severe than average (1963-64), and much less severe than average (1964-65, 1965-66). For most winters it is clear that the period from January through March is the most severe from the standpoint of snow accumulations.

The monthly wind statistics (Table 10) clearly show that wind is quite uniform over the year, and little different during the period of restricted distribution than during other seasons.

The combined effect of wind and temperature has long been recognized as biologically significant, and an index has been developed relating these factors to the comfort and safety of humans. Falkowski and Hastings (1958) define windchill as, "...the cooling power of wind and temperature combinations on shaded, dry human skin."

It is measured in kilogram calories of heat loss per square meter of exposed skin surfact per hour for each Centigrade degree of temperature difference between the skin and the ambient air.

Windchill values were derived from the maximum hourly wind velocities and the corresponding temperatures using the nomogram found in Falkowski and Hastings (1958). A summary of the occurrence of selected levels of windchill is shown in Table 11. The values chosen are described as follows: 800-cold; 1000-very cold; 1200-bitterly cold; and 1400-exposed flesh freezes. Obviously, these descriptions apply directly only to humans, and the projection of windchill levels to effects on deer must take into account their thick winter coat which provides very fine insulation. The summary in Table 11 shows that the more severe levels of windchill occur relatively infrequently in November and April, and irregularly but frequently from December through March.

Distribution and Weather. - Of the several weather factors summarized herein, only temperature, windchill, and snow depth show patterns which appear to be even broadly correlated with deer distribution. Further, measurements made under different shelter conditions in winter clearly indicate little difference in temperatures, but large differences in wind (see next section). The following analysis, is, therefore, restricted to the relationships between distribution, windchill, and snow depth.

The most continuous data on deer distribution were gathered in the winter of 1964-65. From the number of five-chain sections with tracks over the entire track counting route, the percent occurring in the Wolf Lake 140-Catlin Lake 210 division was derived for analysis (this is the only division which includes a traditional deer wintering area). These values for half-month periods from November through April, along with corresponding windchill and snow depth values are shown in Figure 5. The trends strongly indicate that during November and December, and again from mid-March through April, the extent of deer use of this divison was closely correlated with windchill. From January through the first half of March, however, deer use and windchill were not correlated, but snow depth (sinking depth) was.

Some details of the relationship of sinking depth to deer use of concentration areas are shown in Figure 6. This graph is based upon tracks on two separate one-and-one-quarter mile sections of road, one completely in a concentration area, the other outside. From the total number of five-chain sections with tracks in both sections, the percent within the concentration area was derived. These are the values shown in the figure. The general responsiveness of deer to changes in sinking depth is obvious, but the magnitude of the correlation of these data does not appear great.

Distribution Within A Wintering Area

Originally, plans called for the study of deer distribution and activity in a wintering area during the winters of 1963-64 and 1964-65. This plan was followed in 1963-64, but not in 1964-65 when shallow snow depths and much freezing and thawing prohibited effective work. Extensive weather measurements were made in the winter of 1963-64, and intensive weather data were accumulated during the following two winters.

The Wintering Area. - The Deer Creek area, a traditional deer winter concentration area, was selected for this part of the study. The location of this area is shown in Figure 1. The area north of Deer Creek generally faces south, while the part south of the creek faces northwest. Elevations range from approximately 1600 to 1800 feet above sea level, and the topography is relatively gentle. The area is completely forested except for some few small clearings of recent origin. For this study four major forest types were identified, based the magnitude of the coniferous component present. Some of the important statistics pertaining to these types are given in Table 12. Based upon the number of stations (see below) in each type, about 34 percent of the area is in the conifer type (mostly S.A.F. type 24), 40 percent in the conifer-hardwood type (transition type 24-25), 20 percent in the hardwood-conifer type (same transition), and six percent in the hardwood type (type 25). The two transition types have been logged in part, and the nature of the cutting has affected the species composition considerably.

Slightly over two miles of line, marked at one-chain intervals, was employed to record data on the forest types, deer beds, tracks, etc. One-hundred-sixty-seven stations were located and marked for this purpose.

The Weather Stations. - During the winter of 1963-64 temperatures were measured at two stations - one in the hardwood type, one in the conifer type. Snow depth and wind were measured at 17 randomly selected stations over the two-mile route. Snow depth was also recorded at "snow stake" stations in and around the area. During the winters of 1964-65 and 1965-66, recording weather stations were operated to measure temperature, relative humidity, and wind. Stations were located in each of the major forest types, and on the exposed lake adjacent to the area. Some of the characteristics of these stations are listed in Table 13.

Weather in the Wintering Area. - From January through March, 1964, two non-recording maximum-minimum thermometers indicated that both the mean maximum and mean minimum temperatures in the conifer type were about 2°F. lower than in the hardwood type. The mean range (maximum minus minimum) was 2°F. in both types.

Wind measurements made at 17 stations on 13 days indicated that winds of 2 m.p.h. or greater occurred relatively infrequently at a height of 5 feet above the ground in the forest. The maximum ever recorded was 8 m.p.h.; the mean maximum was 4 m.p.h. The average number of stations per day with wind of 2 m.p.h. or greater was four. Often, when the wind in the crowns of the trees was strong, less than 2 m.p.h. of wind was experienced at 5 feet above the ground.

Snow depth means, derived from measurements at 17 stations ranged from 11.7 (+1.1)[1] inches in early January, to 17.1 (+1.9) inches in late February. Snow depth at selected openings around the area averaged between 16 and 17 inches over the winter, as did those in the hardwood type. In the conifer and conifer-hardwood types the average for the winter was 8 inches. Sinking depth means ranged from 14.2 (+1.5) in mid-January, to 2.9 (+0.2) later in the month. Sinking depths in February and March ranged from 7 to 9 inches.

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[1] Figures in parenthesis are those added to and subtracted from the mean to form the 95 percent confidence interval.

From February through early April in 1965, mean maximum temperatures ranged from 33°F. to 35°F. over the five weather stations, while mean minimums were all 14°F. The means of the differences between the daily maximums and minimums ranged from 19°F. in the conifer type to 21°F. on the exposed lake. A trend in these ranges indicated regularly increasing differences from the most sheltered to the least sheltered situation.

Relative humidity varied little between stations, and, in relation to the accuracy of the instruments (5 percent), has to be considered essentially uniform at all stations.

Wind measurements made approximately three feet above the surface of the snow at the five stations varied considerably. A summary of the periodic figures is shown in Table 14. Over the entire period, approximately 11 times more wind occurred on the exposed lake as in the conifer type. Differences between the forested stations were much less, but, overall, nearly twice as much wind occurred in the hardwood type as in the conifer type. An analysis of variance of the periodic averages of the four forest stations indicated that the means differed statistically (F = 4.36, prob. of a larger F .05). Sheffe's test, as described by Edwards (1960), indicated that among the forest stations, only the means for the hardwood and conifer types differed significantly.

A stratified random sample of snow depths in the four forest types was taken twice in January, 1965. Twenty samples were taken in the conifer and conifer-hardwood types, 10 in the hardwood-conifer type, and 5 in the hardwood type. Analyses of variance of these data indicated that the means differed statistically (Table 15). Because the differences in snow depths involved were not considered biologically significant, no attempt was made to determine which individual means differed from one another. This account of the results of the sampling of snow depth is included here solely to illustrate that fairly small differences may be detected with the method employed.

In the winter of 1965-66 only temperature, relative humidity, and wind were measured, and the number of stations was reduced from five to four (the hardwood-conifer station being discontinued). Temperature and humidity measurements commenced in mid-December, wind in January.

Mean maximum temperatures from mid-December through February ranged from 25°F. in the conifer type to 27°F. on the exposed lake. Mean minimums varied from 6°F. on the lake to 8°F. in the conifer-hardwood type. The hardwood and conifer types both averaged 7°F. The means of the differences between the daily maximums and minimums followed the same trend as the previous winter, increasing in order from 17°F. in the conifer type to 21°F. on the exposed lake.

Relative humidity followed the pattern of the previous winter, varying relatively little between stations.

Wind measurements at the four stations indicated a trend similar to that of the previous winter (Table 16), but periodic and overall differences were somewhat less. For example, the exposed lake experienced approximately 8 times more wind than did the conifer type, as compared to 11 times during the previous winter. Also, the hardwood station had approximately 1.2 times the wind of the conifer station, compared to twice as much during the previous winter. Perhaps the fact that two different parts of the winter were involved, i.e., mid-February through early April in 1965, and late January through February in 1966, partially accounts for these differences. The anemometer in the conifer-hardwood type was relocated in 1966 so that it was exposed to more wind. Consequently, more wind was recorded in this type in 1966 than in any situation except the exposed lake. This illustrates the variable nature of wind in the different types, and the importance of the location of the anemometers in relation to local topography.

Track and Bed Counts. - Most of this work was done from early January through mid-March, 1964, when 14 days were spent in the field. Tracks and beds over the two-mile route were tallied and located to the nearest chain along the line. Beds were identified and marked by attaching coded plastic flagging to the nearest tree or shrub. These beds were easily recognized as depressions in the snow resulting from the melting and compaction caused by deer lying down to rest.

Generally, tracks were distributed rather uniformly over the area, but the distribution of beds was restricted and followed fairly definite patterns. Accordingly, beds appeared to be better indicators of the preference of deer for particular situations, and the following account is restricted to the results of the bed counts.

Bed Distribution and Forest Type. - A summary of the distribution of deer beds in the four forest types is presented in Table 17. Clearly, the hardwood type was nearly avoided for bedding, and the conifer and conifer-hardwood types were used extensively. During the entire period these two types contained over 87 percent of all the beds counted, the remainder being in the hardwood-conifer type. In January more beds were found in the conifer type than in all of the other types combined, but during the remainder of the winter the reverse was true. In February and March the conifer-hardwood type alone contained more beds than the conifer type. It should be noted here that both "old beds" and "new beds" are included in this summary, as snow conditions often did not permit an accurate separation of current and older beds.

Bed Distribution and Topography. - A marked change in the distribution of deer beds occurred from January to February. This change is illustrated in Figure 7, where the signed figures are the deviations from the expected scores for each section. The expected scores were derived by distributing the total number of beds tallied during a month over the sections on the basis of equal opportunity for occurrence of bedding. Thus, the positive figures indicate more bedding in a section than would be expected solely on the basis of equal opportunity, and the negative scores less bedding than would be attributed to equal opportunity alone. These figures show that from January to February the distribution of beds changed to consistently favor the higher ground. Bedding declined in all of the sections on higher ground north of the creek (with the exception of one section located in the hardwood type). Even near the creek, bedding increased on a narrow ridge just north of the 180° bend of the stream. An obvious tendency for deer to bed on rises was also observed in February and March.

Bed Distribution and Snow Depth. - The data in Table 17 indicates that when the average sinking depth was 13 and 14 inches, more beds were found in the conifer type than in all other types combined, but as the sinking depths decreased more beds were found in the other types. Thus, at 13 and 14 inches more bedding occurred in the most sheltered type, while below 10 inches as much or more occurred in the other types.

In January of 1965 snow depth was measured at several deer beds in addition to the sampling of the different forest types. On the 20th the mean snow depth (also the sinking depth) in the hardwoods was 8.2 inches, and 6.2 inches in the conifer type, while the mean depth at nine bed sites measured on the 20th and 21st was 5.2 inches. The same relationship prevailed later in the month when on the 29th the means for the hardwood and conifer types were 13.8 and 11.2 inches respectively, and the mean depth at 34 beds measured on the 28th and 29th was 9.5 inches. Thus, even at these relatively shallow snow depths deer were consistently bedding where the snow was the shallowest.

Other Bedding Behavior. - Permanently identified beds were examined periodically in 1964 in an attempt to ascertain the extent of reuse of individual beds. For this purpose the surface of the snow in each bed located on the first day of a series of observations was marked with diagonal cuts made by the blade of an axe. This usually allowed me to determine the next day if the bed had been used in the 24-hour period intervening; if a bed had not been used the marks in the snow would still be clearly visible. If, over longer periods which included significant amounts of snowfall, a bed marked earlier was found to still be in use, it was also recorded as having been reused. Thus, in a coarse way, the minimum reuse of a total of 178 beds was determined. These beds were marked at four different times during the winter - January 16, 28-30, February 15-16, and 25-26.

Thirty and 32 percent of the beds marked in January were known to be reused once by March 12, as were 16 and 8 percent of the beds identified in mid and late February. When these figures are weighted for the length of time that each group of beds was under observation (% reuse/number of days), the resulting reuse indices are all quite similar - 0.54, 0.74, 0.62, and 0.50. The percentages of beds reused twice were 7, 21, 8, and 0, and the corresponding reuse indices are 0.13, 0.49, 0.31, and 0. The only beds known to be reused three times were 4 percent of those identified in mid-January. It should be reiterated that all of these figures are minimal, and that much of the reuse of beds that actually occurred was not detected by the periodic observations.

Snow depths were close to average during the months when these data were obtained, and movement of deer within the wintering area was not unduly restricted. Accordingly, the reuse of beds observed is probably more a reflection of the repeated selection of desirable bedding sites, than of enforced reuse caused by restrictions on movements.

The same general locations were used for bedding in 1965 as in 1964. On the higher ground, with more local relief, specific bed locations were very close together in both years. In the lower shelter areas, where there is much less local relief, bed sites varied more between the years, but many sites were nearly identical in both years.

Distribution of Marked Animals

Observations of marked deer provided limited information on home range, movements, and social grouping. Observations on home range and movements are summarized in this section.

Home Range. - The estimated home ranges of 13 deer are summarized in Table 18. It is readily seen that for the few animals involved, the annual and summer-fall home ranges are essentially one in the same. This means that the winter range is generally a restricted portion of the annual range.

The estimates of the annual home ranges of the adult and yearling deer are remarkably consistent, ranging from 445 to 595 acres. The summer-fall range estimates are more variable, but still may be reasonable estimates due to variations in individual behavior. Thus, in summer some deer are seen in the same small area so frequently, literally day after day, sometimes several times a day, that their actual home range at this time must be very small. Of the deer listed in Table 18, Tommy is the most dramatic example of this type of behavior. However, at this same time of year, other deer may move up to a minimum of 1.8 miles on some days, and others up to 0.7 miles in a matter of hours.

Most of the polygons formed by connecting the outermost points of observation for the individual deer are elongated, with the long axes running generally north and south. All of the ranges so described encompass a variety of vegetation types, and a lake, pond, marsh, or meadow is included in the range of all yearling and adult animals. Some of the summer ranges definitely do not include winter shelter, and are entirely out of traditional wintering range, while other summer ranges not only include winter shelter, but are actually used by deer in winter.

It should be recognized that most of the observations of marked animals were made from the Forest roads, and the configuration of the road system must influence these results greatly.

Most evidence here indicates that generally adult deer occupy the same summer-fall home range year after year, but some deer may not follow this pattern. Thus Mama, an adult doe captured and marked in the summer of 1964, was seen but two times during that summer,but was observed 27 times during the following summer. Either her home range, or the center of activity within that range, changed from one summer to the next.

Movements. - The greatest straight-line distances travelled in a 24-hour period were 1.8 and 1.4 miles, for an adult and yearling buck respectively. Maximum daily movements of does ranged from 0.3 to 0.8 miles, and one adult doe moved 2.3 miles within a week. Over a summer, fall,and early winter period, the greatest distance between observations averaged 1.2 miles.

Frequent observation of some individuals provided data for the calculation of minimum rates of travel during short periods. In 27 observations where deer had moved a minimum of 10 chains (660 feet), rates of travel ranged from 1.90 to 18.18 chains per hour. The mean rate of travel for the 27 observations was 7.59 chains per hour (501 feet), and the 95 percent confidence interval was 5.90-9.28. This result is surprising considering the crude method of observation, and may indicate that the actual rate of travel is relatively uniform.

Emigration. - When marked deer are not seen subsequent to the season of marking, it may be because of lost markings, death, or emigration from the area. In this study I know that some animals lost their markings to the extent that they could no longer be identified as individuals, so that the numbers identified during the second season of intensive observation were minimal. The extent of mortality between the seasons is unknown, but as the winter of 1964-65 was very mild winter loss should have been low. With these limitations in mind the problem of emigration may be approached through the observations of marked deer.

The minimum percent of the deer marked in 1964 which were observed in 1965 is given by various sex and age classes in Table 19. Overall, 43 percent of the deer marked in 1964 were seen in 1965. On the basis of age, 50 percent of the adults and fawns were seen the second year, but only 29 percent of the yearlings. This suggests that emigration may be greater in the yearling class than in the other age groups. This is supported by information on Oscar who was marked as yearling in June of 1964, and remained on the area at least into January of 1965. He was never again seen on the area, and his whereabouts were unknown until he was killed by a hunter in November, 1965, approximately eight miles from his 1964 home range.

Adult animals may emigrate also, which may have occurred with Rasmunda and Cry-baby - an adult doe and her female fawn. These animals were seen regularly throughout the summer and fall of 1964, and again in March of 1965, but never after that time.

All of the results on emigration are based upon a small number of deer, and should be interpreted with caution.

Distribution and Physiology

There appears to be little relationship between the annual sexual cycle and where deer are found, inasmuch as they are distributed quite uniformly from May through November. However, the continuing need for relatively large quantities of plant food for nutrition does influence local distribution, both in summer and winter. Similarly, the "hunger" for minerals in the spring and summer also influence distribution, concentrating numbers of animals in the areas of "licks".

In late winter and early spring deer may remain in sheltered areas beyond the time of severe weather. This may be because of the relatively poor condition of the animals at this time, due to the poor nutrition they have experienced over the winter.

Thus, it seems as if the principal relationships of the deer's physiology to local distribution are based primarily in the related areas of nutrition and condition.

Discussion

The foregoing results are generally in keeping with the existing knowledge of the behavior of white-tailed deer. They do, however, provide some additional insight into some aspects of behavior which are but imperfectly understood, and are therefore worthy of discussion.

Deer are quite uniformly distributed over large areas of the Forest from May through November, but in May, June, and July, some are concentrated in small, local areas which possess especially attractive food or minerals. Other enviromental factors such as shelter, topography, weather, biting flies, and human activity seem to have little influence on distribution during this period, with the exception of weather in November.

The trend toward increased use of coniferous shelter begins in November, and continues through March. Increased use of west exposures begins in December, and also continues through March. During the winter and early spring distribution is not at all uniform, and deer favor sites with the most coniferous shelter, and west aspects. During January, February, and March, areas lacking an abundance of these sites may be completely deserted by deer. It should be noted, however, that the intensive deer use of west aspects may be somewhat misleading, as many of the sections so classified are really nearer to southwest, and provide good exposure to the sun from mid-winter through early spring.

The trend toward increased use of the coniferous shelter types began in November, before snow depths were sufficient to impede mobility. During November and December the relative use of the area containing an abundance of continuous coniferous shelter was closely correlated with the number of hours with windchill of 1200 or greater, and this same relationship held for the period from mid-March through April. During January and February deer use of the wintering area was not closely correlated with windchill which remained very high, but rather followed the changes in sinking depth in the snow cover. Throughout the two winters with relatively shallow snow depths, deer responded promptly to changes in sinking depth produced by snowstorms, rains, thaws, and the formation of supporting crusts. I believe the foregoing evidence suggests the hypothesis that trends toward the initiation and ending of winter concentration are strongly influenced by regularly increasing and decreasing levels of windchill in the late fall and early spring, and that during the winter, when windchill is consistently high, the degree of concentration is most influenced by sinking depth. That windchill, rather than low temperature alone, is the climatic factor of genuine importance ininfluencing distribution is apparent from the weather measurements made in the Deer Creek wintering area.

These results seem to clearly indicate that if shelter is indeed sought to mitigate the effects of severe weather, the principal factor involved is windchill. This is because temperature relationships are essentially uniform in situations which vary tremedously in shelter value. Not only is the coniferous shelter no warmer on the basis of temperature alone, it may be slightly colder (although somewhat more thermally stable), than other situations. Wind, however, is considerably less in the conifer type, and windchill must accordingly be less there than in the more exposed situations. For example, at 0°F. windchill is approximately 900 at 2 m.p.h. of wind, 1100 at 4 m.p.h., 1375 at 10 m.p.h., 1500 at 15 m.p.h., and 1600 at 20 m.p.h. (exposed human flesh freezes at 1400). Thus, the advantage of deer locating themselves in areas where the wind is minimum during cold periods is obvious, and the least wind occurs in the coniferous shelter areas.

The observations of the distribution of deer beds in the wintering area also indicates the preference of the animals for coniferous shelter in winter. In the two forest types which contained over 87 percent of all of the beds recorded the coniferous crown cover averaged 50.8 and 62.3 percent, as compared to 29.3 percent for the type which contained essentially 100 percent of the remainder of the beds. The crown cover at the actual bedding sites was even higher than these figures for the types. These results compare closely to those of Gill (1964) who indicates that in Maine most bedding sites have a minimum of 40 to 50 percent crown closure, with the leading crown class being 41 to 70 percent. In the Deer Creek wintering area the mean softwood basal areas for the types most used for bedding were over two and three times that of the next most used type.

The preference of deer for bedding under dense coniferous crowns means that they bed quite consistently where the snow is the shallowest. Measurements here indicated that the individual beds are in snow that is even shallower than the average for the conifer type. This is probably the result of the preference of the animals for bedding under sizeable coniferous trees. In Maine, Gill (1964) found that the center of the largest bed at the typical bed site was four feet from the bole of a spruce of at least 8 inches d.b.h. This tendency is also evident here, and may mean that a favorable micro-climate is afforded by such conditions. The boles of sizeable trees may serve to reduce air movement over the animals, but hardwood trees should serve just as well in this respect as softwoods. Also, the snow under hardwoods is generally deeper, and should provide more insulation to bedded animals than the shallower snow under softwood trees (des Meules /1964/ describes this phenomenon in moose). Gill (1964) doubted that the preference of deer in Maine for coniferous cover in winter could be attributed entirely to behavior oriented toward the conservation of body heat, and his remarks (p. 11) on this subject are worth quoting.

> Some aspects of deer behavior which the findings suggest are also intriguing. For example, the well-known tendency of deer to bed under a large softwood tree and to travel "from tree to tree" even when not handicapped by deep snow, implies that some winter behavior has been conditioned by factors that are not exclusively related to physical comfort or conservation of energy. Need for psychological security is probably involved. Further understanding of such factors might help explain the fairly frequent questions concerning areas which seem to have all the ecological characteristics associated with deeryards but which are not used by deer.

The results of this study strongly indicate that these thoughts apply here as well as in Maine.

Food appears to influence distribution of deer in winter only if it is available in concentrated abundance (the same may be said of the summer season also). This is generally restricted to logging areas where quantities of food are available from the tops of felled trees. These tops may, in addition, provide increased low-level shelter from wind, but to my knowledge no studies of the shelter values of actively logged areas have been made.

The general consensus is that deer are somewhat indifferent to food in winter (see the review of Verme, 1965), orienting their behavior almost solely toward shelter which reduces the effects of severe weather. I believe that this is an oversimplication of the situation, and that at any season deer will respond intensively to food only where it occurs in concentrated abundance. This is true here even in summer, when deer are widely distributed in general, and concentrate only where food supplies are very concentrated (see details on aquatic feeding behavior, Chapter VI). Moreover, the value of food in winter in the absence of protecting shelter would be of dubious value except where occurring in very concentrated abundance. Thus, when deer are said to ignore range with plentiful browse in winter in favor of sheltered areas low in food, this may mean that what is plentiful to the observer is not plentiful enough to the deer.

The data on ranging of marked animals appear to give reasonably consistent estimates of home range. These data are too few to attempt to explore the complex question of home range in detail, but some points should be noted. Foremost is the fact that almost all of the observations contributing to these results were made from the Forest road system and undoubtedly are influenced by the configuration of the roads. What part of the areas enclosed by the polygons is actually used by the individual deer is not known, but frequent and numerous observations of some deer were made in small areas within the entire home range. This indicates that some portions of the home range must be used far more than others, and during the summer at least, there may actually be centers of activity within the overall home range.

Deer in regions of marked climatic change from summer to winter are often thought to occupy quite distinct summer and winter ranges. This is doubtless true in some areas, but here it appears that during winters of average or less than average snow depths deer winter on a restricted portion of their summer-fall ranges. I believe this is a reflection of the good distribution of coniferous shelter areas over the Forest, which makes large movements to and from winter range unnecessary. This has probably been the case in this immediate locality for about the entire time that deer have been numerous.

Too little information on movements of marked animals off the area is available to warrant a lengthly discussion of emigration. If the indications of these sparse data are accurate, however, it appears that at least as many (and probably more) adults and fawns remain on the area as leave. More yearlings, on the other hand, appear to leave the area than stay. Nothing is known of immigration to the Forest, so the net effect of movement on and off the area cannot even be crudely estimated.

The full implication of these findings in relation to management are difficult to state concisely. The following comments therefore represent the most important generalizations on this subject.

In this region, where the winter climate is severe, coniferous shelter in winter is required, except possibly where food is concentrated in abundance. Large areas of coniferous shelter, however, do not appear to be required, or even desirable.

The relatively uniform distribution of smaller coniferous shelter areas over the Forest appears to result in relatively small seasonal movements of deer, which means that a large portion of the population may be considered resident the year round. From the standpoint of intensive management, this seems to me to be clearly preferable to situations where deer move long distances from one seasonal range to another, and where large winter concentrations often results in a tremendous depletion of the food supply in and around wintering areas.

When silviculture is considered, the widespread distribution of deer over most of the year is probably a mixed blessing. Thus, while the potential detrimental effects of browsing damage to valuable timber species is widespread, this may be preferable to the heavy damage which may result in areas where deer are concentrated. The local concentrations of deer in areas of very abundant aquatic food in summer may result in heavy damage to tree reproduction in surrounding areas when the aquatic food has lost its attraction (see Discussion of Aquatic Feeding Behavior, Chapter VI); and the concentrations in and around areas of coniferous shelter in winter definitely prohibit adequate regeneration of some valuable species, e.g., yellow birch, while favoring species that are not eaten, e.g., red spruce.

The findings on distribution definitely apply to the management of deer for recreational viewing. Most of the demand for such viewing is in the summer when distribution is uniform except for very local concentrations. But while deer are literally "everywhere" during the summer months, they cannot be seen with equal facility in all areas. This is clear from the observations of deer in June, July, and August, when the section of road associated with the meadows produced from 200 to nearly 350 more observations per month than the section of road through the essentially continuous forest. Another section of road devoid of meadows, but possessing many clearings, produced 534 observations of deer in the three summer months, compared to 84 for the coninuously forested section. Clearly, manipulation of the environment to provide openings, and the location of roads to take advantage of open areas such as meadows, can provide tremendously increased opportunities for viewing deer in summer.

The local food and mineral concentrations which attract numbers of deer in spring and summer could also be important in this respect. Green herbage and mineral attractants along regularly-travelled highways are undesirable, as deer use these areas principally after dark, creating a hazard for motorists, and an apparently incurable temptation for jack-lighters. Concentrations of animals off the highway, however, at salt licks, and in areas of abundant aquatic food can greatly enhance the opportunity for observation of deer. This subject is discussed further in Chapters V and VI.

CHAPTER V

ACTIVITY

Review of the Literature

The subject at hand is not where deer are found, but rather how active they are at different seasons; and, during shorter periods, how activity is affected by environmental factors, chiefly weather. Before proceeding directly to the literature dealing with deer, some general points are worth examination.

Cloudsley-Thompson (1961 b) states that Park distinguishes two types of rhythmic phenomena: exogenus rhythms - responses to changes in the environment which do not persist under constant conditions; and, endogenus rhythms - or those which continue, at least for a time, under constant conditions. The latter may be sub-divided into inherent and habitual rhythms. While endogenus rhythms may not be in response to environmental factors, they are frequently correlated with them. The activity of most animals in their natural environments is effected by a composite of endogenus and exogenus rhythms.

Barnett (1963, p. 20), who has studied the behavior of both wild and laboratory rats (Rattus norvegicus), says of activity:

> Activity in rats, measured in a wheel, in a maze or in more open space, is increased by three kinds of stimulation. First, changing environmental stimuli, acting on the exterocepters, increase activity. Second, some kinds of constant environmental stimulation, such as bright light, do the same, since in general bright light is avoided. Third, deprivation, for instance of food, (a) lowers the threshold of response to external changes, (b) may itself increase activity in a constant environment.

Thus, it should be obvious that activity in the higher animals is the result of a complex of interacting environmental and physiopsychological factors which may be difficult to document accurately, let alone explain.

Seasonal Patterns

There is a paucity of information on seasonal activity patterns in wild mammals, and deer are no exception. Accordingly, this review is brief, but includes what little is known of seasonal activity, and of physio-morphological changes which occur in deer seasonally.

Very few definitive studies have documented seasonal activity in deer. Miller (1965), in a year-round study of a confined herd of black-tailed deer, recorded the most sightings in May, the least in January. This could presumably, be an indication of differences in activity level at different seasons. Progulske and Baskett (1958) believed that seasonal shifting of home ranges might have accounted for the progressive decline in the number of both marked and unmarked white-tails observed from late summer to January, but it seems possible that declining activity could produce essentially the same result. Montgomery (1963, p. 425), reporting on nocturnal activity of deer in Pennsylvania, presented information which I interpret to mean that deer become progressively less active at night from summer through winter. Progulske and Duerre (1964) found that increasing numbers of deer were seen at night from early August through mid-September. Michael (1965) found that some white-tails in Texas ranged over more area in winter, others more in summer. But ranging may, or may not, be a reasonable indicator of activity. In red deer, Darling (1937) found that movement was least in December and January, and greatest in May and June.

The relationship, if any, of these physiological phenomena to seasonal activity levels in deer is presently unknown.

Short-Term Activity

Daily Patterns. - Severinghaus and Cheatum (1956) state that opinions differ as to whether the white-tail is essentially nocturnal, diurnal or crepuscular. Merriam (1886) believed that while deer are generally thought of as nocturnal, their daily acitivity was greatly modified by environment, resulting in nocturnal activity in areas much-frequented by man, and diurnal activity in more remote areas. In their summer observations in the Adirondacks, Townsend and Smith (1933) found much evidence to support Merriam's view, with much local variation in activity. Considerable daytime activity was observed in some areas, little in others. They believe that collectively deer show little regularity in their feeding hours, except for a general preference for evening. They concluded that, where undisturbed, deer may be more crepuscular than nocturnal.

In central New York, where, unlike the Adirondacks, considerable human activity occurs, Cook and Hamilton (1942) found that deer in winter remained bedded during the day, and commenced to feed an hour or two before sunset. Kabat, et al. (1953) found deer in a Wisconsin yard most active during the hour before sunset and least active between 9:00 A.M. and noon. Montgomery (1963) thought that people working on his study area may have caused deer to remain bedded in the woods during the day, presumably explaining the high activity at night when there was little disturbance. He describes the pattern on his study area in central Pennsylvania as follows (p. 425):

> Nearly all deer on the area were active during all seasons for a period lasting from 1 to 2 hours before sunset until at least 1 hour after sunset (Fig. 2). Following this period of activity, progressively more deer bedded, until a peak in the relative numbers of bedded deer was reached during the night. In summer, the peak of bedding occurred 7-8 hours after sunset (just before dawn), and nearly all deer were active at dawn. In fall, the first peak of bedding occurred about 5 hours after sunset, and in winter about 4 hours after sunset. In winter, some deer became active for a short time after the first peak of bedding, but many were again bedded about 6 hours after sunset.

In South Dakota in summer, Progulske and Duerre (1964) observed that deer moved into meadows to loaf and feed after sunset, but did not remain there throughout the night. Eighty-two percent of the deer they observed were seen within five hours after sunset, and nearly 79 percent within a four-hour period starting one hour after sunset. Chapman (1939) found most daytime activity of deer in southeastern Ohio occurred between sunrise and 10:00 A.M. and between 5:00 P.M. and sundown, but probably the most activity occurred at night. In Texas, Halloran (1943) found white-tails active in the morning, afternoon, and evening: but when morning and evening counts were both made, two to three times as many deer were seen in the evening as in the morning. Severinghaus and Cheatum (1956) state that most deer feed during early morning and late afternoon, with a preference for evening. They point out, however, that this is an average condition, and that some deer can be seen feeding during daylight hours, while some feed at night, particularly in areas where they are harassed by man.

Lord (1964, p. 41) studied the seasonal activity patterns of captive cottontail rabbits (Sylvilagus floridanus). He found that cottontails, which are essentially nocturnal, "...increased duration of activity during the summer months when nights were the shortest...". He suggested that, "It is possible that in some species daily activity is maintained solely by endogenus rhythms geared to sample physiological processes, such as the length of time required to assimilate a given quantity of food." He concluded by suggesting, "...that the process of food assimilation, more complicated in herbivores than in carnivores, may provide the endogenus clock for regulating the daily activity pattern of rabbits, and possibly other herbivores."

Day length is the only seasonal environmental factor ordinarily considered regular enough in nature to govern many regularly-occurring morphological or physiological phenomena. French, et al. (1960) studied the response of white-tailed bucks to added artificial light. Experimental animals were subjected to a constant 16 hours of light per day, while that of the controls varied from 10 to 12 hours. Increased light advanced both the spring and fall pelage changes by about three weeks, and advanced both the onset of rutting and the shedding of antlers by about two weeks each.

Silver and Colovos (1957), citing others, suggested that physiological changes associated with hours of daylight, could result in reduced food consumption in winter, and not to prepare the deer for the traditional semi-starvation period. They also noted that through the use of artificial light, the basal metabolism of three Holstein heifers was increased 23 percent (vs. 0.06 percent for controls). McEwen, et al. (1957) found that captive deer ate less in winter than at other seasons, and suggested, "...that seasonal metabolic changes may have evolved as a means of adaptation to winter food scarcity." Silver (1962) first indicated a progressive increase in the basal metabolic rate (BMR) in captive white-tailed deer from late winter to mid-summer. Her subsequent reports have presented additional evidence to support this view, and to permit the formulation of the hypothesis of regular seasonal changes in the BMR of deer (Silver, 1963; Silver, et al., 1965; Silver, 1965 b). The progressive increase in BMR from winter to summer, measured for one doe in different years, took place irrespective of the influence of food, growth, and pregnancy. The most recent evidence presented by Silver (1965) shows not only an increase in BMR from late winter through early summer, but a regular decrease from mid-summer through October.

Silver (1965 b) has also reported dramatic differences in the reaction of deer to environmental temperature both while moulting and in the summer coat, as opposed to that while in the heavy winter coat. Critical temperatures for deer moulting or in the thin summer coat were much higher than for animals in the winter coat. She thus poses the question - "Does this lack of body insulation contribute to the high BMR we have consistently observed in the spring?"

Browman and Sears (1956) have found similar cyclic variation in the thymus gland in all age-classes of female mule deer, with a good correlation between average monthly hours of daylight and thymus volume/body weight curves. They suggest the hypothesis that light stimulates the production of a thymotropic hormone, probably via the pituitary. The pituitary, among many functions, controls the rate of thyroxin from the thyroid gland, which acts to stimulate the chemical activities of the body and thus produce a rise in the basal metabolic rate (Etkin, 1964). Etkin continues to say that in this way it (the thyroid) probably plays a significant role in the seasonal adjustments to temperature change.

The foregoing review of daily patterns deals almost wholly with white-tailed deer, but the patterns of other species also deserves mention for comparison. Cronemiller and Bartholomew (1950) observed that mule deer were not active at midday during the warmer months, but were generally active for a large part of the day in winter. Taber and Dasmann (1958) found black-tailed deer active at all times during June and July except during midday, when they bedded. Miller (1965) recorded activity peaks in this species as follows: (1) January and February - midday; (2) March-May - early morning; (3) June-August - slight in late morning, higher at twilight; (4) September - high in morning, slighter at twilight; (5) October - early morning and midday; (6) November - high throughout the day, peaking at midday; and, (7) December - high mid-morning until twilight.

de Vos (1960) reports that during the summer, caribou are active at all hours of the day and night, except for a slight inclination to rest in the darkest hours. He found peaks of activity from 10:00 A.M. to noon, and from 2:00 to 5:00 P.M., Harper (1962) found the daytime activity of elk (Cervus canadensis) influences by weather, but generally following a morning - evening pattern. Cronemiller and Fischer (1946) observed numbers of deer (species not given) in California and southern Oregon throughout the day from sunrise to dusk, but found the greatest numbers from sunrise to noon, and from 6:30 P.M. to dusk. They stated: "The relationship of weather to the effectiveness of the counts in this area appeared to be of less importance than the time of day." The importance, or supposed importance, of weather in governing activity is reviewed in the following section.

The Effect Of Weather On Activity

While few studies have been made of the effect of weather on deer activity, many biologists have recorded their observations during the course of other studies. The result is interesting, but often confusing. In order to provide a broader base for discussion, this review, in addition to dealing with several species of deer, has been expanded to include some other mammals.

It is tempting to order this review on the basis of sections dealing with individual weather factors, but this would require tedious repetition of many citations. I have, therefore, chosen to review all factors for a species, or a group, together.

White-tailed Deer. - Banasiak (1961) says that in winter, activity within deer yards is increased on warm days, and when snow crusts support the animals. He indicates that deer are less active under the following conditions; (1) high winds and low temperatures; (2) storms; (3) breaking snow crusts; and, (4) when sinking depths are more than 18 to 24 inches. Day (1963) found that during very cold periods (-22^{o} to -26^{o}F.) activity was reduced to a minimum, and that fresh tracks were seldom seen far from bedding areas. Severinghaus and Cheatum (1956) observed that on cold nights (-20^{o} to -30^{o}F.) few deer were bedded, while most walked slowly along trails, whereas on warmer nights most deer were bedded. They suggested that the reduction in activity under more moderate temperatures might "...indicate less need for exercise to maintain body heat and ward off chilling." Conversely, Silver and Colovos (1957), reported that in periods of extreme cold (-30° to -32°F.) penned deer appeared to make every effort to avoid heat loss by lying down and remaining nearly motionless. On the coldest mornings, some shivered when aroused. Under such conditions the deer remained uninterested in food, even when it was warmed. They suggested that at excessively low temperatures, deer may be unable to eat enough to offset the heat losses entailed in gathering, warming, and digesting food that is as cold as the surrounding air, and that conservation of heat may offer the best chance for survival. Of the response of their deer to shelter they said (p. 22):

> There was no shelter except the open pens inside the barn. Ordinarily the deer made more use of them to escape the heat of summer than the cold of winter, and unless the wind was blowing they usually slept outside even during storms. After a snowfall they appeared like mounds in an unbroken field of snow, and when they came in to feed the melted snow remained on their backs, often several inches thick, until they shook themselves.

Tester and Heegan (1965) found that January movements of white-tails were considerably larger in warmer periods than during periods of extreme cold.

Townsend and Smith (1933) observed deer activity around Adirondack Lakes in summer, and found greater activity on comparatively warm days, either cloudy or clear, windy or calm, than on cool days. Heavier showers seemed to drive deer to the shelter of the woods, and on rainy days practically no animals were seen. Lowering temperature during the day also resulted in low activity. Chapman (1939) found that more deer were feeding on cloudy, rather than clear nights, and on calm rather than windy ones. Cool nights were favored slightly over warm ones, and a strong preference was shown for rainy nights. Daytime activity was influenced by sky conditions, deer being active throughout the day when cloudy, but inactive between about 10:00 A.M. and 5:00 P.M. on clear days. Barick (1952) found that deer in North Carolina appeared to feed more heavily just prior to low pressure storms, and that more deer were active on clear, moonlit nights than cloudy ones. However, he recognized the possibility that better visibility for the observer on moonlit nights, rather than high activity, could have accounted for this result.

In Texas, Halloran (1943) found that morning and evening activity of white-tails was positively correlated with temperature. More deer were seen when the sky was overcast, and there was little or no wind. Hahn (1949), on the other hand, found that deer were most active on cloudless days of low relative humidity. He concluded that the best weather for counts of deer was when the relative humidity was below 70 percent, and the sky was not more than 50 percent overcast. Hahn also observed that temperature, atmospheric pressure, and wind had no appreciable effect on movements. It should be noted here, however, that due to the considerable negative correlation between temperature and relative humidity, if either one is highly correlated with deer activity, the other must, by definition so to speak, be correlated with activity too, though not necessarily to the same extent. In Michigan, Van Etten, et al. (1965) reported that more deer were seen by hunters in a square mile enclosure on "good" days, than at other times.

In South Dakota, Progulske and Duerre (1964) made continuing counts of deer (about 90 percent white-tails and 10 percent mule deer; Progulske, pers. comm., July, 1964) in meadows at night. Using multiple and partial correlation techniques, they found that 85.28 percent of the variation in the counts could be attributed to cloud cover, temperature, precipitation, dew, and relative humidity. Partial correlations of each of these factors with deer seen were significant, with temperature apparently exerting the most influence. Temperature and relative humidity showed positive correlations, whereas cloud cover, precipitation, and dew showed negative correlations. As temperature and relative humidity were significantly correlated (negatively), it is difficult to understand how they could have both been correlated positively with deer seen.

Mule and Black-tailed Deer. - Russell (1932) found that drops in temperature, and early fall snowstorms were coincident with a restlessness in mule deer on their upper summer range. In Colorado, Wright and Swift (1942) observed that mule deer slowed their migration during periods when temperature dropped, especially when stormy weather accompanied the decrease in temperature. Cronemiller and Bartholomew (1950) found mule deer in the chaparral forests of California active on frosty spring mornings until the sun warmed the air. They remained active up to midday on cool days, as opposed to about 10:00 A.M. on warmer days. In winter, they found deer active for a large part of the day when the weather was not too inclement. In summer, Dixon (1934) found mule deer feeding mostly before sunrise, in the late afternoon, and after sundown, and spending midday bedded down in cool places. In Colorado, Loveless (1963) observed mule deer throughout the daylight hours under a wide variety of conditions. He found that decreased activity was related to temperatures of 45° to 50°F. and above, accompanied by very dry atmospheric conditions. Rain or snow, independent of other weather, had no effect on deer, but snowstorms accompanied by low temperatures and high winds induced the deer to seek shelter. Loveless concluded that deer response was seldom induced by independent environmental factors operating alone, but that response to weather was, "most closely associated with, or induced by, high air temperature and low atmospheric moisture, low air temperature and low atmospheric moisture, low air temperature accompanied by high winds or high atmospheric moisture or both,...".

Black-tailed deer in California were found to prefer temperatures between 55° and 65°F. in summer, and were active in the morning, late afternoon, and throughout the night (Taber and Dasmann, 1958). In Oregon, Miller (1965) found inactivity above 60°F. did not occur until weekly maximums remained consistently above 60°F. In winter, he observed that when temperatures dropped below 20°F. the deer stayed bedded until mid-morning, and that overall activity was reduced. Sudden drops in temperature after sunset (8° to 19°F. within one hour) sharply reduced activity. During periods of high precipitation (January-March; November-December) relative humidity had no effect on activity, but in April and May activity increased sharply as the minimum relative humidity fell steadily. In October, when minimum relative humidity was rising consistently, activity was greatly reduced. During the rainy season Miller found deer equally active during heavy or light rains, but in drier periods heavy rainfall resulted in greatly reduced activity. If rain persisted for more than a day, activity increased somewhat while the rain continued. When the rains ceased, activity increased suddenly, and remained at high levels for several hours. McCullough (1964) felt that the direct effect of precipitation on black-tails was slight, and that its primary importance lay in its influence on temperature and relative humidity. As indicated earlier under Distribution, he found that both the spring and fall migrations were initiated in relation to cumulative minimum relative humidities (for five to seven day periods) of between 40 and 60 percent. Apparently, he observed no daily effects of relative humidity on activity.

Other Cervids. - Murie (1951) indicated that while storms may drive elk to shelter, many feed in the open during storms. Hard winds however often cause them to seek shelter. He also observed that in the spring elk are susceptible to heat, and often seek cool places. Dalke, et al. (1965) made similar observations, indicating that cover was sought more on warm, sunny days in spring and summer, than during winter. They also found that elk were more active during adverse weather than during mild weather. Harper (1962) also found elk more active on rainy days, or when the barometer was falling. Temperature also affected activity, with feeding commencing and terminating earlier on hot mornings than on cool ones. On hot days the evening feeding period was similarly affected.

Darling (1937) stated that movement was one of the chief means by which higher animals maintained themselves within fairly wide ecological normality. In his studies of red deer in Scotland, he found weather exerting considerable influence on movements, and his findings are worthy of careful review.

Of temperature, Darling said that deer, "...do not mind cold, qua cold; they may even seek it." He found that sudden cold, however, brought deer downhill, and restricted their daily movements. Daily movement was least in December and January when there was the least variation between maximum and minimum temperatures, and greatest in May and June, when the range of temperatures was the widest. He suggested that deer may be more sensitive to changes in temperature in spring and summer due to shedding, and the thin summer coat. Movement of red deer was always toward conditions of most even temperature.

Darling found humidity an important factor in the behavior of deer. He believed that broadly speaking, high humidity tended to restrict activity, and a dry atmosphere induce it. Under conditions of variable humidity, he found deer irritable; due, he believed, to constant olfactory stimulation. When humidity was more constant, deer were less irritable. Darling stressed the importance of humidity and temperature in affecting the transmission of scent through the atmosphere.

Similarly, wind was considered important mainly as a vehicle of information through the transmission of scent. Direct effects of winds of less than gale force were negligible, but gales in any season resulted in the deer seeking shelter, or moving downhill.

Rain did not appear to influence movement greatly, but steady rain restricted it, while thunder and lightning did not appear to disturb the animals. Snow, however, influenced movements profoundly, with dramatic movements and grouping of animals preceding storms by one or two days. Darling was impressed and baffled by the foreknowledge of these storms by the deer. As barometric pressure was found to have no consistent relationship to movement, the explanation of the deer's foreknowledge of bad weather evaded him. To my knowledge, it has not been explained to this day.

de Vos (1960) found that winds over 25 miles per hour seemed to induce bedding in caribou, and that following adverse weather the animals seemed to feed more actively. Yazon (1961) found that elk (probably Alces alces) in Russia reacted much differently to cold weather at different times. Except during migration, they spent most of the time reacting, and fed for only one to two hours a day. Conversely, during migration, the elk were most active on severely cold days.

Other Mammals. - Limitations on space prohibit a complete survey of the influence of weather on the activity of all mammals. The following is but a brief summary of some interesting papers on this subject that have come to my attention.

Next to deer, probably more has been written of weather and rabbit activity, than of any other mammals. Hanson (1944) found that high activity in cottontails was associated with high barometric pressure, low activity with low pressure, but concluded that it was daily changes in pressure, rather than absolute highs and lows, that were most highly correlated with activity. He indicated that this relationship was most pronounced in January and February, and was vague and contradictory in early winter. Statistical analysis failed to confirm this correlation. Johnson and Hendrickson (1958) also found that in winter cottontails were more active during or after a rise in barometric pressure, and when snow was on the ground (as compared to when the ground was snow-free), but multiple correlations were not statistically significant. Newman (1959) also employed multiple and partial correlation analyses of roadside rabbit activity and weather factors, and found that snow on the ground was the only factor which was significantly correlated with activity. Other factors, which were not found statistically significant, were: wind - negative; cloud cover - none; and, heavy fog and light mist - positive. Voris (1956) reported that summer activity of cottontails was negatively correlated with wind, and that other factors showed no correlation. Alkon (1965), employing simple correlation coefficients, found negative correlations between rabbits seen and temperature, wind, moderate to heavy rain, and heavy fog, and positive correlations between activity and dew, light fog, and light rain. No correlation was reported for activity and relative humidity, cloud cover, or barometric pressure. In Australia, Rowley (1957) found rabbit (Oryctolagus cuniculus) activity in the evening was disturbed most commonly by wind and rain, and that bad weather (or heavy predation) the previous night, could affect activity the following evening.

Packer (1965) observed that different weather patterns at different seasons were associated with high activity in the quokka (Satonix brachyuras), (the quokka is a small, macroped marsupial of western Australia, nocturnal in habit). In his summary, Packer states, (p. 282):

> During the dry part of the year (October to March),high activity is generally associated with falling barometric pressure which directs a flow of warm, dry, easterly air over the study area. During the wetter part of the year (April to September), high activity is often associated with heavy rainfall; however, the animals appear to prefer non-rainy nights and hence are more active under clearing conditions with rising barometric pressure and cooler temperatures.

The response of predators to weather should at least be mentioned. Saunders (1963) found that captive lynx (*Lynx canadensis*) were less active during rain and snowstorms than during good weather. Conversely, Storm (1965) found that movements of two free-ranging red foxes tracked by telemetry were not restricted by rain and snowfall.

The activity of small mammals has been of interest to several investigators including Pearson (1960), Getz (1961), and Osterberg (1962). Results with regard to weather factors have shown much variation among different groups and species.

The foregoing clearly indicates that the relationship of weather factors to activity levels of mammals in general, and of deer in particular, is a complex affair. Animals react differently to some weather factors in different environments, and at different times of the year. Studies which show the most consistent results are generally those employing statistical correlation, e.g., those of cottontail rabbits. To my knowledge, no controlled studies ot confined deer have been made, and but one employing multiple and partial correlation to examine activity of free-ranging deer and weather relationships has come to my attention. Thus, what has been recorded of activity and weather has often been incidental to other field studies, and consequently the results are difficult to interpret at best, and often confusing.

Other Factors And Activity

Few definitive statements are available concerning the influence of factors other than weather on deer activity. Indeed, almost all that can be done is to infer the effect of these other factors from their stated effect on distribution. Accordingly, this review is extremely brief, and given only to illustrate that other factors must be recognized.

Darling (1937), for example, cites both insects and food supply as influencing movements of red deer. While his statements on insects and deer movement are restricted to distribution, I infer that activity as evidenced by movement, was restricted at times of peak biting fly activity. Darling also points out that while predators of red deer are absent in Scotland, where present, predators often keep deer moving. Progulske and Baskett (1958) found that harassment of white-tails by hounds occurred during all seasons in Missouri, and that deer were sometimes driven long distances.

The relationship of physiological and morphological factors to deer activity is documented only indirectly. Severinghaus and Cheatum (1956, p. 119), state: "The summer season for deer is quiet, lazy time. The bucks are being careful of their ultra-sensitive growing antlers, and the does are tending their young." Clearly, the inference is that some aspects of the reproductive biology of deer result in relatively low activity in summer. They continue to describe the habits of the white-tail during the rut, indicating a period of relatively high activity. They also postulated (p. 145) that following heavy snowstorms in the Adirondacks those deer that were in good physical condition could remain bedded longer, utilizing their stored energy, whereas the weaker, hungrier animals were required to break open trails to seek food.

Age may also be related to activity in young animals. Michael (1965) observed that white-tail fawns in Texas, spent most of their first two months of life bedded; after that time they accompanied their mothers.

Results

Seasonal Activity Patterns - Time And Weather

The pattern of deer activity throughout the year as indicated by 91, 24-hour accumulations of tracks is shown in Figure 8. Three major periods are evident in this pattern: (1) winter - when there is no trend of activity with time; (2) March-October - when a regular and rapid increase in activity occurs from March through June, followed by a regular but more gradual decrease through October; and, (3) mid to late autumn - when a rapid increase in activity occurs from late October through early December, followed by a decrease to the variable activity of winter. The analyses of these periods, and the characteristics of activity within them, form the substance of this section.

Several multiple correlation analyses were employed to examine the quantitative associations between deer activity and select environmental variables. In these analyses the simple correlation coefficients (r) provided estimates of the correlation between deer activity and each independent variable without regard for the other variables. The partial correlation coefficients, however, estimate the correlation between activity and an independent variable with the other variables held constant. The multiple correlation coefficient (R) in each analysis provided an estimate of the correlation of activity with all of the independent variables combined. This coefficient squared - R^2 - provided an estimate of the percent of variation in activity which may be attributed to the independent variables in combination. The quantity $1-R^2$ indicates the percent of variation in activity not attributable to the variables under consideration, hence attributable to other factors.

The statistical significance of the simple and partial correlation coefficients was determined by appropriate use of the t-distribution, and the multiple correlation coefficients by use of the F distribution. In all cases the null hypothesis was that the population correlation equaled 0. A significant test statistic ($P = .05$) resulted in the rejection of the null hypothesis of 0 correlation, and the alternate hypothesis, i.e., the population correlation was not equal to 0, was accordingly accepted. All of the following statements of statistical significance, or of non-significance, are based upon the acceptance or rejection of these hypotheses.

March-October Activity. - The results of the multiple correlation analysis for track counts within this period are shown in Table 20.

A high positive correlation between hours of daylight and the track count scores is evident, with both the simple and partial correlation coefficients being significant.

Neither maximum daily temperature nor minimum daily relative humidity shows consistent correlations with the track counts, as the simple correlations are significant, but the partials are not. Thus, when day length is held constant, neither of the measures of temperature or humidity was correlated with deer activity for the 24-hour period.

The multiple correlation coefficient (R) is also significant, and the R^2 of 0.76 indicates that 76 percent of the variation in the track counts may be attributed to the three independent variables in combination. This is scarcely higher than the r^2 for tracks and day length alone (0.74), indicating that 74 percent of the variation in activity may be attributed to day length completely independent of other factors. Or, stated another way, day length alone accounted for as much variation in the track counts as the variables of day length, temperature, and humidity together.

Days with heavy precipitation could not be included in this analysis as rain obliterated tracks and made counts untrustworthy. Other observations indicate that deer do not avoid activity during brief periods of rain, even heavy rain, but prolonged precipitation does depress activity. No marked trends of activity with cloud cover, or with changes in barometric pressure were noted, but deer were often active just prior to, or during the early stages of a storm.

Late Spring and Summer Activity. - Spot lighting and track counts were employed to examine some characteristics of deer activity during this period. Figure 9 shows the results of 47 spot lighting counts made from 11:00 P.M. through 1:00 A.M. from mid-May through August in 1965. A variable, but gradually decreasing trend in nighttime activity is evident from these data.

The results of multiple correlation analyses for selected counts are shown in Table 21 and 22. The first analysis (Table 21) indicates that the day of observation from late May through August is negatively correlated with numbers of deer seen, as both the simple and partial correlations are significant. Neither temperature nor wind during the counting period shows significant correlations with numbers of deer counted. The R is significant, and the R^2 indicates that 74 percent of the variation in the deer counts may be attributed to the combined effects of the three independent variables. This is but 10 percent greater than the r^2 for number of deer seen and day of observation alone (0.64). Thus, the day of observation, which herein is closely correlated with day length, clearly accounts for most of the variation in nighttime deer activity throughout the summer.

In order to include different levels of relative humidity in a multiple analysis of activity and weather, the weather occurring four hours prior to the spot lighting period was used. This was required because relative humidity during the 11:00 P.M. to 1:00 A.M. period was usually at or near saturation. The results of this analysis are shown in Table 22. A negative correlation between number of deer seen and day of observation is evident as both the simple and partial correlation coefficients are significant. Among the weather variables only the partial correlation coefficient for deer seen and temperature is significant, indicating a positive correlation. The R is also significant and the R^2 indicates that 69 percent of the observed variation in numbers of deer seen may be accounted for by the independent variables in combination. This is 20 percent more than can be accounted for by the r^2 for deer seen and day of observation alone (0.49).

I think these results strongly indicate that from late May through August, nighttime activity is more closely associated with the day of the season (or day length), than with weather conditions. Moreover, the evening weather is more closely associated with nighttime activity than is the weather during the hours of darkness. This view is supported by the observations of activity on nights with precipitation (excluded from the multiple analyses for standardization). Generally, rain in the evening resulted in few deer being seen during the 11:00 P.M. to 1:00 A.M. counting period, while rain immediately before and during the spot lighting period did not appreciably affect activity.

No marked relationships between deer seen and moonphase, cloud cover, fog, thunder, lightning, or barometric pressure were noted.

Simple correlation analyses were used to compare nighttime activity measured by both spot lighting and track counts during different summers (Table 23). The track counts are for a 12-hour period from 6 P.M. to 6 A.M., and the spot lighting counts from 11:00 P.M. to 1:00 A.M. All of the negative correlation coefficients between activity and the day of the season are significant and homogeneous, and confirm the trend of decreasing nighttime activity throughout the summer. The correlation between the percent of the 24-hour track score in the 6:00 P.M. to 6:00 A.M. period and the day of observation is of particular interest. It indicates that nighttime activity decreases in relation to total daily activity from late May through September. Conversely, the relative amount of activity during the 6:00 A.M. to 6:00 P.M. period increases throughout the summer and early fall.

The details of activity levels during shorter periods within a 24-hour day are difficult to measure with track counts, but some counts of 4-hour accumulations of tracks during daylight hours were done. The results of these counts in 1964 are shown in Figure 10. No marked pattern of activity during these days is apparent. Moreover, the limited data show no consistent evidence of a midday lull in activity commonly associated with deer during the summer.

A more detailed account of daytime deer activity in summer is furnished by data obtained at Deer Lake in 1964 and 1965. Deer activity at this lake is closely associated with the abundance and condition of aquatic food, and generally heavy use of the lake occurs from about mid-June through early to mid-August (see Chapter VI for details).

The pattern of daytime activity at the lake is shown in Figure 11. These results clearly show that activity rises throughout the morning until about 11:30 A.M., then remains essentially constant through 3:00 P.M. Extended observations in the late afternoon and evening indicate a gradual decrease until dusk, and very little activity occurs after dark. The observations of numbers of deer counted during the middle of the day (11:00 A.M. - 3:15 P.M.), when activity is uniform, were employed in the multiple correlation analyses shown in Table 24.

The negative correlations between deer counted and day of observation are lower than in the preceding analyses, but all of the coefficients except the partial for 1964 were significant. Relative humidity and number of deer seen were consistently negatively correlated for both years with all coefficients being significant. None of the partial correlation coefficients for deer seen and temperature, or activity and wind were significant. In 1964 the R was significant, in 1965 it was not. The R^2s indicated that the independent variables accounted for 52 and 22 percent of the variation in deer activity in 1964 and 1965 respectively.

These results indicate the trend of decreasing activity during the summer as shown by the spot lighting and track counts, but the correlations are less marked. This is probably due to the confounding factor of the concentrated aquatic food which attracts deer to the lake (see Chapter VI). Relative humidity is clearly negatively correlated with midday activity on the lake, and this, by definition, implicates temperature, which is itself negatively correlated with relative humidity (r's - 1964 - 0.50, 1965 - 0.30; both significant). However, relative humidity is clearly more closely associated with activity than is temperature, as of the partial correlations only those for deer seen and relative humidity are significant.

Activity at the lake was generally lowest on rainy days, intermediate on cloudy days, and highest on clear and partly cloudy days, but measurements of light in 1964 were not found to be correlated with activity.

One interesting aspect of deer behavior on the Forest which occurs consistently year after year, is manifested in the rapid decline in observations of deer along the roads during late summer. The sharpest decline occurs between late August and mid-September, when observations reach a seasonal low (Figure 12, week 36). The track count estimates of activity also decline at this time, but the decrease is more gradual, and the low is not reached until mid-October (Figure 8, week 39). Deer thus appear to be more difficult to observe in late summer than the general level of activity would indicate. This may be due to changes in behavior alone, or, may also be influenced by the change from the red to the gray coat which makes standing deer more difficult to detect.

Autumn Activity. - The pattern shown in Figure 8 indicates that activity is low in September and most of October, then rises sharply in late October to peak in late November before falling off into the irregular pattern of winter. From late October through November activity closely coincides with the intensity of the rut, and except for storms, appears to be independent of weather.

Winter Activity. - Deer activity during the winter proved to be exceedingly variable, and followed no discernible pattern over time (Figure 8). Several weather factors appeared to influence activity, but varying distribution during the winters of 1964-65 and 1965-66 due to changing snow conditions made meaningful analysis difficult. In order to minimize the effects of these changes in distribution, only the months of January and February were employed to investigate correlations between activity and weather.

For January and February simple correlations were examined between activity (tracks) and temperature, relative humidity, wind, windchill, and sinking depth. Of the measures examined, only maximum daily temperature proved to be significantly correlated with the scores of the 19 track counts used ($r = 0.66$). Scatter diagrams showed that activity and windchill were probably negatively associated, but the correlations were not significant.

A limited multiple correlation analysis of the 19 track count scores, maximum daily temperatures, and sinking depths showed that the simple and partial correlation coefficients for activity and temperature, and the multiple correlation coefficient (R) were all identical and significant (0.66). Thus, both R^2 and r^2 equalled 0.44, indicating that 44 percent of the variation in activity could be attributed to temperature alone, and that sinking depth contributed essentially nothing to the analysis.

The positive relationship between winter activity and temperature was further confirmed by the analysis of feed consumption of a penned yearling male on 48 days the latter part of November, 1963, through January, 1964. The significant positive correlation coefficient was 0.32.

Track counts could not be completed accurately when much snow fell during the 24-hour period of track accumulation. However, bed and track counts made in the Deer Creek wintering area showed that activity was somewhat less on days with or immediately following a snowfall, than on days not associated with snowfall. Severe snow or ice storms definitely depressed activity.

Seasonal Activity - Biotic Factors

No marked relationship between deer activity and changes in food or cover could be discerned at any season.

Samples of biting flies taken during the summers of 1964 and 1965 showed little correlation with deer activity either on the Forest roads or at Deer Lake (see Chapter VI).

Human activity appeared to have little effect on deer activity as measured by the track counts. For example, during the late spring and summer, activity rose, crested, and fell while human activity over the Forest roads was consistently high. Deer activity also increased then decreased during the fall when human activity was consistently moderate. Thus, at all seasons, deer activity levels appeared to be independent of the magnitude of human activity on the Forest.

Seasonal Activity - Morphological And Physiological Factors

Several morphological and physiological conditions of the deer are associated with prominent portions of the activity pattern described in Figure 8. First, the dramatic increase in activity from April through mid-June coincides closely with the spring moult from the heavy winter to sparse summer coat. The peak of activity in late May and June occurs during the height of the fawning season. The subsequent gradual decrease in activity generally coincides with the nursing period, and the latter part of this decline also coincides with the autumnal moult from summer to winter coats. Finally, the sharp rise in activity from late October through November occurs as breeding activity increases.

Discussion

The activity pattern shown by the March-October analysis, and supported by the summer analyses, has never, to my knowledge, been reported before. The strong correlations between deer activity and day length (or date) suggest a well-developed pattern with a firm physiological basis in which day length is the primary stimulus. There is a body of evidence from other studies that this physiological basis does exist.

McEwen, et al. (1957) found that captive deer ate less in winter than at other seasons, and suggested, "...that seasonal metabolic changes may have evolved as a means of adaptation to winter food scarcity." Silver and Colovos (1957) suggested that this behavior was associated with varying day length, and cited increases in the basal metabolic rate (BMR) of cattle induced by added light. French, et al. (1960) found that bimonthly feed consumption by captive white-tails varied almost directly with average monthly temperatures, and concluded that this was as expected as the warmest days occurred during the period of greatest daylight, and the coldest during the time of least daylight. Silver (1962) first noted a progressive increase in the BMR of captive deer from late winter to summer, and recently has shown that a regular decrease in BMR occurs from mid-summer through October (Silver, 1965). The progressive increase in BMR from late winter to summer occurred in one doe studied in different years entirely irrespective of the influences of food, growth, and pregnancy (Silver, et al., 1965).

The pattern of the BMR in captive deer in New Hampshire is strikingly similar to the seasonal activity pattern found on the Huntington Forest, and the similar latitudes of the study areas, about 43°20N. and 44°N. respectively, would indicate a very similar regimen of daylight throughout the year.

Correlations *per se* cannot imply cause and effect, but indirect evidence strongly suggests the probable nature of the relationships involved. Browman and Sears (1956) found that the size of the thymus gland in mule deer was positively correlated with day length, and suggested that light, acting through the pituitary, stimulates the production of a thymotrophic hormone. The same basic mechanism is suggested by Etkin (1964) for control of the thyroid gland which, through the production of thyroxin, controls metabolism. The seasonal changes in metabolism and activity in white-tailed deer which are so closely correlated with day length are probably manifestations of this process.

The entire annual activity pattern cannot be explained this simply however, as the fall breeding season is a period of high activity which occurs as day length decreases. Wislocki (1943), who examined the annual sexual cycle in male white-tails, concluded that the breeding season is the culmination of the entire sexual cycle which is initiated in the spring on increasing light. He hypothesized that the primary control of the breeding cycle was accomplished by light acting on the pituitary, which in turn acted on the gonads. French, et al. (1960) actually advanced the onset of the rut in captive bucks by adding artificial light. I conclude that light is intimately associated with the sexual cycle, but that the mechanism by which regulation is effected by both increasing and decreasing day length is not clear.

Light is also associated with both the spring and fall moults (French, et al., 1960). Silver (1955) has found dramatic differences in the reaction of deer to environmental temperature while moulting and in the summer coat, as opposed to that while in the winter coat. Critical temperatures were much higher for deer moulting or in the summer coat, than for those in the winter coat. She thus poses the question - "Does this lack of body insulation contribute to the high BMR we have consistently found in the spring." Darling (1937) found more movement in red deer in May and June when wide ranges of temperatures coincided with moulting and the assumption of the thin summer coat. On the Huntington Forest the highest period of activity is also in May and June and coincides closely with the spring moult which is ordinarily completed in mid-June.

The foregoing strongly suggests that seasonal activity is closely associated with varying day length, which, acting as a primary stimulus, may induce physiological changes which result in changes in metabolism. Metabolism may in turn, be influenced by environmental temperature, which is a more potent stimulus when deer are moulting, or in their thin summer coats. The precise relationships among these factors have yet to be determined.

The apparent influence of weather factors on deer activity is not as striking as that of day length. Other than the depressing effect of storms, only humidity and temperature appear to be important. Recent studies of black-tailed deer have indicated that periods of consistently decreasing relative humidity coincide with increases in deer activity (McCullough, 1964; Miller, 1965). Darling (1937) found that low humidity induced day to day movement in red deer, while high humidity restricted it. Hahn (1949) saw more white tails in Texas when the relative humidity was low than on more humid days.

The results of daytime observations during the summer are consistent with the evidence that activity and humidity are negatively correlated, and that the correlation is stronger than the positive one between temperature and activity. The humidity pattern over the year however, is not correlated with activity, and in this region probably humidity is of little importance to deer activity except as it may effect day to day activity during the warmer months.

Temperature and activity were found to be positively correlated in winter, and this is in general agreement with other observations of white-tails on northern ranges (Silver and Colovos, 1957; Banasiak, 1961; Day, 1963; Tester and Heegan, 1965). Silver and Colovos describe behavior which they believe indicates that deer actually attempt to conserve body heat by lying down, erecting hair, and remaining essentially motionless. The general positive correlation between temperature and nighttime activity in summer agrees with the observations of Progulske and Duerre (1964).

It is commonly accepted that high temperatures act to depress daytime activity in summer. The results of the observations at Deer Lake do not agree with this belief, as activity was high throughout the midday period in warm weather. Further, the four-hour track counts do not indicate lowered activity during the warmer parts of the day in summer. Probably the specific nature of the temperature regimen in different regions governs the response of deer to high daytime temperatures in summer. In the central Adirondacks extended periods of high temperature during the day are uncommon, and the short period of heat during the day are uncommon, and the short period of heat during most summer days is probably insufficient to induce inactivity.

The lack of positive association between other weather factors and activity is certainly not conclusive, but it appears very unlikely that factors other than storms and wind influence activity significantly. Storms clearly depress activity, and wind, acting in concert with cold winter temperatures may do the same. A multipoint sampling system which actually provides measurements of wind velocity is needed to even begin to determine the quantitative relationships between activity and wind, or windchill.

The implications of the findings on activity are diverse, and may be of interest to both the zoologist and wildlife manager. Certainly deer managers and researchers who work with enumeration of deer through drives, track counts, and other techniques, must recognize that changes in activity can greatly affect their estimates of populations, and take such changes into account when planning their work and evaluating their results. An appreciation of the relationship of some of the important weather factors to activity at different seasons is also required to plan and interpret deer and track counts.

The high activity of the late spring-summer period provides great opportunity for intensive recreational viewing of deer along forest roads. The low activity in late summer and early fall precludes the opportunity for viewing animals easily, but suggests the possibility of providing additional hunting opportunity by opening the season as early as mid-September without appreciably increasing the kill.

The seasonal relationships between deer activity, basal metabolism, and food consumption may have profound biological and management implications. If these relationships are sustained, we will have evidence of yet another species which has evolved a valuable physiological adaptation which better fits it for its environment. Further, game managers should evaluate their winter habitat management plans with this in mind, recognizing that perhaps they can do no more for deer in winter than to create conditions which foster more uniform distribution.

Silver and Colovos (1957) have asserted that, "Sound management can only be achieved through a thorough knowledge of how deer live, and a year round appraisal of the range they live on." While management based on incomplete or superficial knowledge will not necessarily result in failure, it may at best, prove to be much more complicated and expensive than is actually required.

CHAPTER VI

ADDITIONAL ASPECTS OF BEHAVIOR

Three other aspects of behavior are considered in this chapter. These are: (1) social behavior; (2) aquatic feeding behavior;and, (3) response of deer to human disturbance. The last is very limited in scope, as most of the intensive phases of the work were transferred to a master's degree thesis program which is scheduled for completion in May, 1966.

Social Behavior

Review Of The Literature

The work on social behavior included herein is limited in scope, and, accordingly, this review is limited to those aspects of behavior actually observed.

Etkin (1964 b) defines social groups as those whose members stay together as a result of responses to one another, rather than as a result of responses to other factors in the environment. In white-tailed deer the only social group for most of the year has been thought to be the family group, i.e., the mature doe with her newest fawns and at times, her fawns of the previous year (Severinghaus and Cheatum, 1956). Chapman (1939) says that groups in summer consist of does with their newborn fawns of the previous year, both male and female, and small groups of bucks. These bucks, and others which live singly, seldom associate with does. Severinghaus and Cheatum (1956) indicate that family groups breakup with the advent of the fawning season, but that when the newborn fawns are able to travel with their mothers, there is a tendency for the yearlings to rejoin the group. Hawkins (1965) noted that after the family breakup in May-June, the following trends were found: (1) adult does associated primarily with their young fawns until October-January; (2) yearling siblings, except those that fawned, remained together until October-November; (3) yearling bucks were never associated with their mothers again; (4) yearling does that had fawns followed the same behavioral patterns as adult does; and, (5) yearling does and their fawns (if any) rejoined the adult doe and her fawns from October to January. Some weaker associations were observed between some adult does, and between a few adult, and yearling bucks. Associations of marked animals that Hawkins observed most frequently were, in order of occurrence, fawn-fawn, adult doe-fawn, yearling-yearling, adult doe-female yearling, adult doe-adult doe (same ages), adult doe-adult doe (different ages), and adult buck-adult buck. Michael (1965) observed that male fawns remained with their mothers for at least a year after birth, female fawns at least one-and-one-half years.

Another aspect of social behavior involves dominance and aggression. Davis (1964) states: "The major function of aggressive behavior is to determine and maintain rank or territory." In some species, aggressive behavior is most often associated with the sexual activity of males. Cowan and Geist (1961) state that in cervids the most intensive behavior is that which accompanies the sexual excitement of the males. This may consist of actions direct at the inanimate environment, other males, or toward females. Among captive white-tails, Severinghaus (1955) reported several instances of fatal attacks on unreceptive females by bucks during the rutting season.

Non-breeding aggression and dominance are also manifest in deer. Severinghaus and Cheatum (1956) state that there is an obvious tendency toward group dominance by larger deer, bucks, or does. Kabat, et al. (1953) found that the dominance order established at a winter feeding station was generally males - females - fawns, with the larger deer dominating. Deer were generally intolerant of each other while feeding, and fighting with hooves was common. Severinghaus and Cheatum (1956) report similar winter behavior in the Adirondacks. Robinson (1962) reported on dominance relations among penned white-tailed deer fawns. He found that in general, heavier animals dominated, and that males tended to dominate females. Strange fawns were found to fight with their forefeet upon meeting, and once an animal was beaten it remained subordinate. Once the dominance order was thus established, it was maintained. Robinson noted that strife was probably more prevalent in the pens due to artificially high densities than it would be in the wild.

Results

Group Size and Composition. - Roadside observations of marked and unmarked deer were recorded to document grouping tendencies over the seasons. The observations on group size for all deer seen are summarized in Table 25. The most striking aspect of these results is the pronounced trend in the observations of single deer, where a regular decrease in the percentage of sightings occurs from June through April. In May the trend reverses sharply, climbing to the high in June. Observations of four-six deer display an opposite trend, with the lowest percentage in June, the highest in April. Observations of groups of two and three deer also follow this trend, but with somewhat less regularity.

Similar trends are also evident in the more detailed record of observations of various sex and age combinations (Table 26). These figures show that relatively more females are seen alone in June than in any other month, and that the lowest percentage of groups including does are observed then. The subsequent decrease in observations of single deer (excepting males), and increase in observations of various groups, is less regular than that of group size only (Table 25), but the trends are essentially similar.

In addition to these trends, several other details of the results are worth noting. These are: (1) the abrupt increase in the percentage of observations of single deer from April to May, and from May to June; (2) the particularly low-level of group observations, and female-female sightings in June and July; (3) the increase in observations of two deer, and of does and fawns from July to August; (4) the relatively infrequent, but consistent observations of male-male sightings throughout the summer; (5) the abrupt increase in observations of single males from October to November; and, (6) the consistently high percentage of observations of four-six deer throughout the winter and early spring.

Observations of marked deer, made mostly in summer and fall, indicate that some deer are seen alone much more frequently than others. However, when the marked animals were seen with other deer, there was considerable uniformity in the size of the groups. These group means range from 2.00 to 3.00, with most ranging from 2.25 to 2.67. While the size of the groups is relatively uniform, the individuals comprising some groups may vary considerably at times, and from day to day different combinations of marked and unmarked animals have been observed. Thus, in addition to the continuing associations, there appears to be some temporary contacts in summer and early fall.

Observations of some marked deer seen alone and with other marked and unmarked animals are summarized in Table 27. The bulkof these are summer and fall observations. These results are quite variable, due possibly to the small number of deer involved, and the grouping of the data over several months. Accordingly, interpretation is difficult, and firm generalizations impossible to make. Thus, the following comments simply represent a summary of my current impressions.

Adult females are more often observed alone than with other deer in summer (but in 1965 Tommy and Anna-K were exceptions to this pattern). Yearlings, conversely, are seen more often with other deer, usually other yearlings. In the late summer, and fall, some yearlings may rejoin the family group, as evidenced by the frequent sightings of Rasmunda (doe) and Cry-baby (fawn) with a spike-horn believed to be a yearling. In summer, females and yearlings are seldom seen with adult bucks, and the one marked adult male (a six-pointer) was always seen alone, or with other adult males.

Qualitative observations of deer feeding at Deer Lake in summer follow patterns very similar to those described for marked deer.

Aggressive Behavior. - Most of the observations of aggressive behavior were made of wading deer feeding at Deer Lake during the summers of 1963, 1964, and 1965. Being largely incidental to other work, these observations were not recorded in a quantitative manner, and the following comments are thus entirely qualitative in nature.

The most singularly striking fact that emerges from these observations of large numbers of deer at the lake, is that there is relatively little visible conflict and aggression in summer. The most frequent meetings of "strange" deer occur as the animals wade in opposite directions, close to shore, where they often pass with no visible indication of recognition. In these situations, however, large does and mature bucks are often given wide berth. Mature males appear to be very tolerant of one another, and from two to five large bucks may feed near each other in a relatively small area. Occasionally, upon leaving the water, two or three well-developed males will stand very close together, with no apparent hostility. Not infrequently, two or more large bucks will emerge from the woods together, and feed close to one another. These males are, however, almost completely intolerant of other deer, including some males of lesser stature. Occasionally these smaller males, but more often yearlings of either sex, approach, and even attempt to sniff a large buck. The usual response of the buck is a rapid lowering of the head, followed, if necessary, by a lunge toward the intruder, who is quickly repulsed, usually without physical contact. Occasionally, a buck may repel an intruder by rising up on his hind feet instead of by lowering his head.

Quite different conditions prevail when several deer congregate in a small area to feed on uprooted water shield that has been accumulated close to shore. These aggregations are made up almost exclusively of does and yearlings. As they wade back and forth, and in and out while feeding, close approaches to each other are frequent and strife is more common. The visible aggression is usually executed by a large doe, which drives away closely approaching deer by lunging, or, more often, striking at them with her forefeet. These encounters, which may or may not involve physical contact, are extremely one-sided, with the smaller deer always fleeing from the doe, rather than replying in kind.

Discussion

Deer on the Huntington Forest appear to follow the general patterns of grouping described for white-tails by Severinghaus and Cheatum (1956) and Hawkins (1965). The family groups apparently begin to separate in May, and by the fawning season (late May-July) most adult females are seen alone or with their newborn fawns. Yearlings of both sexes are more often seen alone or with other yearlings. Adult males are almost always seen alone, or with other adult males. The size of the groups increases from August through the winter, indicating that some yearlings rejoin the family group, and that some older deer may continue to be associated with such groups. In relation to the annual activity pattern described in Chapter V, deer appear to be more social during seasons of low activity, i.e., early fall, winter, and early spring, than during the time of high activity - late spring and summer. The fall rutting period is, of course, the one exception to this pattern. The seasonal changes in the basal metabolic rate described by Silver (1965 b), may be related to changes in social grouping behavior, with the higher metabolism of summer resulting in higher activity and more independent movement. However, while the correlations appear to be strong, there is no evidence to suggest a cause and effect relationship.

The observations of marked deer during the summer and fall indicate that some groupings are not completely fixed, but that different animals may join and leave some groups periodically, affecting their composition and size. This may be broadly similar to the behavior of kangaroos (Macropus spp.) described by Caughley (1964), in which the size of groups is determined by an essentially random process of animals joining and leaving.

The limited observations on dominance and aggressive behavior in summer, generally follow the patterns described for white-tails at winter feeding stations (Kabat, et al., 1953; Severinghaus and Cheatum, 1956). Thus, generally, larger deer dominate smaller deer, and males dominate females. The striking impression, however, is of remarkably infrequent displays of aggression and dominance during the summer. This is made especially apparent by the compatibility of adult males at this season. Summer is also the time of highest metabolism and overall activity, but as in the case of groupings of animals, nothing can be reasonably suggested at present to explain the correlation in causal terms.

Aquatic Feeding Behavior

Review Of The Literature

Very little is found in the literature pertaining to the details of aquatic feeding behavior in white-tailed deer. Merriam (1886) mentions that deer in the Adirondacks feed on aquatic plants but gives no details. Seton (1937) also mentions the attraction of white-tails to aquatic plants, citing the roots, stems, and leaves of lily-pads as favored food. More information is given by Townsend and Smith (1933), especially on species of plants eaten. They also include very brief descriptions of the characteristic feeding behavior of wading and swimming deer.

Results

The daily and seasonal activity patterns of summer deer use of Deer Lake, and the relationship of weather to these patterns have been described in Chapter V. Here, we are concerned with some of the details of what the deer are doing at the lake.

Early in this study it was apparent that two environmental factors, i.e., abundant biting flies and abundant aquatic food, could account for the concentration of deer at the lake in summer. Systematic samples of blackflies (mostly Simulium spp.) and deerflies (mostly Chrysops spp.) taken in 1964 indicated that from three to 45 times more biting flies are found in the adjacent upland, than along the exposed lakeshore. However, no significant correlations were found between daily biting fly abundance and daily deer use of the lake in either 1964 or 1965. In 1965, moreover, there was not even a weak trend between flies and deer use of the lake. Both qualitative and quantitative observations did indicate, however, that deer use of the lake was closely associated with the abundance, distribution, and condition of the most sought after aquatic food, water shield.

Deer use of the lake rises in June with the increase of the water shield, generally peaking in late June or early July. In 1964 use of the lake declined steadily from early July through the end of the month, and was essentially over by the beginning of August. In 1965, however, intensive use of the lake was fairly stable throughout July, declining slowly through August. The difference between these years (about 45 versus 75 days of intensive use), is probably directly attributable to differences in the condition of the water shield, which was heavily damaged by insects in 1964, but remained essentially intact in 1965.

Some idea of the density of water shield in several sections of the lake in 1964 can be had from inspection of Table 28. In spite of removal of considerable quantities of this plant by deer during the last half of June and the first half of July, the overall mean density of floating leaves was six times greater in August than in early June.

Deer were systematically tallied as feeding or not feeding when first observed during 1964. Of 745 observations, 542 were of feeding animals. Analysis based on numbers (1) wading and feeding, (2) wading and not feeding, (3) swimming and feeding, and (4) swimming and not feeding, produced a highly significant chi-square ($X^2 = 63.4$; significant at $P = .01$) indicating that the use of the lake by deer is not independent of feeding. Feeding by swimming deer was particularly striking, with 182 of 192 (95 percent) observations in the feeding class. Actually, when extended observations are made, all swimming deer are found to feed, as are most wading deer.

Distribution of deer around the lake also appears to be closely associated with the distribution of water shield, with sections containing the most food generally having the most use. In addition, deer tend to concentrate in areas where quantities of water shield, uprooted during periods of high wind, have been washed in close to shore. Under these conditions, individual deer may spend nearly all of their stay on the lake in a very limited area.

Four reasonably distinct feeding patterns have been observed at the lake. A brief description of these patterns follows. (1) Swimming-feeding - Deer that follow this pattern usually enter the water immediately upon emerging from the woods, and proceed directly to deeper water where they feed almost continuously on water shield. The duration of the swimming and feeding ranges from about two-and-one-half minutes to over an hour, with the larger deer generally swimming longer than smaller animals.

Males and females follow this pattern approximately in proportion to their occurrence on the lake. Adult females may swim alone, or with yearlings. The younger animals do not appear to feed as continuously as the adults while swimming. Animals that swim for a relatively long time, usually leave the lake directly upon returning to shore. (2) Standing-feeding - Animals that follow this pattern enter the water up to their briskets or backs, and stand and feed on both emergent and floating leaved vegetation, moving only to keep in an area of abundant food. This pattern is more prevalent in adult males than in other deer. Often large bucks will stand and feed in depths where smaller deer must swim. Upon leaving the water these bucks stand on shore for some time before entering the forest. (3) Shoreline wading, continuous - In this pattern, animals usually begin to wade along the shore as soon as they have entered the water. As they wade along, they pick up pieces of water shield, especially bits of stems, and occasionally stop for short periods to eat bunches of bladderwort that have been uprooted and washed-in close to shore, or to browse on shoreline shrubs. This pattern appears to be more variable than the preceding two, and at times is combined with number 4 (below). (4) Wading, limited - This pattern is often followed by single animals that usually wade back and forth in a limited area feeding mostly on aquatics, and to a lesser extent shoreline shrubs. Where considerable amounts of uprooted water shield have washed ashore, numbers of deer may congregate and follow this pattern.

In 1965 observations were made at 15-minute intervals to record activity levels, and in addition, the number of swimming and non-swimming deer were tallied. The frequency distributions for the observations made from 11:15 A.M. through 3:30 P.M. (EDST) are shown in Figure 13. The distributions for all deer and for non-swimming deer resemble normal distributions, but the distribution of swimming observations is highly skewed to the left, with the great bulk of observations in the 0 and 1-2 classes. Thus, it seems that in good weather some deer are at the lake at all times, and that numbers at any observation period follow an approximately normal distribution. However, larger numbers of swimming deer are seldom observed, and the bulk of these observations range from zero to two.

In order to document some of the quantitative aspects of swimming-feeding behavior, swimming periods were timed with a stop-watch. The frequency distributions of these observations are shown in Figure 14. It can be seen that the pattern for adult males differs greatly from the pattern for other deer. The distribution for males is generally rectangular, while that for other deer is highly skewed to the left. The descriptive statistics for these swimming periods shown in Table 29 serve to illustrate some of the details of the differences between the swimming periods of males and other deer. Due to the significant disparity in the variances of the two groups (F = 3.76, probability of a larger F 0.01), statistical analysis beyond inspection of the descriptive statistics is probably unwarranted. Clearly, the length of the swimming period is more variable for males than for other deer, and on the average considerably longer.

Almost all deer feed continuously on water shield while swimming, following a course which keeps them within the "beds" of vegetation. Variable, and sometimes complicated (for the observer to follow) routes are thus followed by many swimming deer.

Discussion

These results provide a spectacular illustration of the profound influence of an abundant, and apparently palatable, food supply on deer behavior. Moreover, they show that behavior within an area of abundant food is sufficiently adaptable to take full advantage of the desired food. Further, the evidence strongly supports the position that deer enter the water principally to feed, and that relief from attacks of biting flies is largely an incidental benefit.

It is well known that deer swim (Severinghaus and Cheatum, 1956), but swimming has been attributed almost entirely to a means of traveling from one place to another, or to harassment by hunters or dogs. Only Townsend and Smith (1933) mention deer swimming and feeding. Results here, however, clearly show that deer will freely enter the water to wade and swim, in order to avail themselves of desirable food. As deer are poorly equipped structurally for swimming, or even wading on soft bottoms, I interpret this behavior as further evidence of the considerable behavioral adaptability of the species.

One particularly fascinating question remains to be answered. Is the heavy use of water shield by deer simply a result of a concentrated and palatable supply of food, or is there some aspect of the chemical composition of the plant, or the lesser plants and animals which occur on it (algae, etc.), which prompts this behavior.

The possible management implications of these findings are diverse, but somewhat nebulous, and perhaps are currently best phrased as questions. First, should desirable aquatic vegetation be managed to encourage or to discourage summer concentrations of deer? Once the attraction of the aquatic food wanes in late summer, do deer concentrated in the general area then produce unusually heavy damage to desirable tree reproduction in adjacent forests? Finally, can and should these summer concentrations of deer eventually be managed for recreational viewing by vacationers and tourists?

Response To Disturbance

Much of the work originally planned for this part of the study was transferred to a master's degree thesis program. Accordingly, for a more detailed account of summer flight behavior of white-tails, the reader should consult the work of Lubeck (1966, in press).

Review Of The Literature

To my knowledge, no meaningful information on the response of white-tailed deer to disturbance is available in the literature. Other work in this area of behavior is pertinent however, and is included here.

Hediger (1955, p. 41), who pioneered the concept of flight distance - the distance to which an animal can be approached before it flees - states:

> The animal adapts its flight behavior to the specific circumstances of its surroundings. Thus, for example, in the national reserves (in Africa), where man does not appear as a hunter, flight distances are usually less than in hunting areas.

The work of Altmann (1958) provides an excellent illustration of these points in cervids. Altmann found that several factors influenced the flight of elk and moose in Wyoming. She summarized these factors as follows: (1) a seasonally changing threshold of sensitivity due to reproductive and nutritional status; (2) variations due to type of habitat; and, (3) variations due to specific experience of the individual or the group. Moose cows with newborn calves were found to have short flight distances, while cows with heeling calves had much longer flight distances. Bulls in velvet had long flight distances, rutting animals very short ones. During the hunting season the flight distance was very long. In winter, flight distance decreased, due, in Altmann's opinion, to a general lowering of vigor, and to difficulty in moving fast in deep or crusted snow. In open country flight distances were longer than in timber, but water-feeding moose had shorter flight distances than those feeding on land. Wind direction and strength, fog, weather noises, and level of daylight all influenced the distance to which moose could be approached. Altmann also found that under certain conditions moose can give a reversed reaction to disturbance. Thus, in a meadow much frequented by tourists, moose were found to be highly suspicious of silent approaches under cover, taking flight at long distances, while noisy tourists could approach them closely. She also reported thatwhere humans are seldom seen, elk show little fear of people.

Results

Many people made observations of deer incidental to their other activities, and it was thus impractical to attempt to record flight distances. Accordingly, tail position in flight was selected as an indicator of the response of deer to disturbance. Here white-tails in full flight usually run with their tails raised high, while in lesser flight the position of the tail varies, but is often held down. Only the results of those observations in which deer clearly fled with their tails up or down are reported here. A partial summary of these results is shown in Figure 15.

The graph shows only the percent of animals which fled with their tails up; a graph of animals which fled with their tails down would simply show the opposite trend. An obvious trend in these data occurs from March through November, with the percent of deer fleeing with their tails up decreasing from March through July, and increasing from July through November. If tail position in flight is a reasonable indicator of the reaction of deer to disturbance, this indicates a less violent response in summer than in other seasons.

While flight distances were not measured in this study, some qualitative observations are worthy of mention. Generally, deer here can be approached closer by vehicle in the late spring and summer than during other seasons. Deer wading in the water can often be approached by canoe more closely than those on land can be by vehicle, but swimming deer are very difficult to approach and invariably flee as soon as they detect any disturbance. Generally, deer can be approached more closely by vehicle than by foot, and more readily after dark than during daylight hours. Occasionally, I have approached deer who were clearly aware of a disturbing presence to a distance of about eight feet while they drank water at a salt lick at night. This close approach was allowed despite the fact that the animals appeared somewhat disturbed by my movements and the occasional light from my flashlight.

Discussion

Hediger (1955) recognizes the raising of the tail or the erecting of the hairs of the rump patch in flight as an escape signal in many hoofed mammals. He stresses, however, that contrary to popular belief, the signalling animal warns others entirely without intention. de Vos (1960) reports that caribou raise their tails in reaction to alarm, and this type of behavior is also recognized in many large mammals. However, to my knowledge, nothing is known of the details of such behavior.

The results of this study appear to indicate that in white-tails the position of the tail in flight, while most often up, varies considerably and regularly over the year. During the summer, when flight distances are relatively short, nearly as many deer flee with their tails down as up. At other times, when flight distance is generally longer, more deer flee with their tails up than down. This is particularly pronounced during the rutting season, which, on surrounding lands, is also the hunting season.

One qualifying observation should be made at this point. The data in Figure 15 include observations of all ages and both sexes of deer. I think this makes little difference regarding sex, but young fawns differ markedly from other deer in that during the summer, once they are able to run well, they invariably flee with their tails up. This is so even when a fawn follows a doe who is running with her tail held down (I take this to mean that the tendency to flee with the tail up is inherent in the species, but that the habit is modified by experience). This means that the tails up percent figure for July is probably somewhat higher than it would be for older deer only, and that the August figure may be considerably higher.

Thus, it seems clear that deer on the Forest do react differently to disturbance at different seasons. The less pronounced reaction in summer may be due to the reluctance of does to leave their young fawns. Yet many of the observations of deer fleeing with their tails down are of unaccompanied does, yearlings, and bucks. Also, the regularity of the trend cannot be explained on this basis. The increased cover provided by the leaves of deciduous plants in summer might increase the animals sense of security, and thereby account for the summer behavior. However, this could hardly account for the trend from March through November.

The regularity of the trend in tail position almost required that a physiological basis be considered. As the trend appears to be highly correlated (negatively) with seasonal changes in activity and basal metabolism, it may be that some related physiological change influences flight behavior. The high metabolic rate of summer, however, would probably result in more irritable behavior than that at other times, and if it was related to flight behavior, tend to produce results contrary to those recorded.

Finally, it must be conceded that the meaning of the position of the tail in flight is unknown. It may, or may not be meaningfully related to the flight behavior of white-tails. This question, and the entire area of response to disturbance, appear to offer good prospects for fruitful future study.

CHAPTER VII

SUMMARY AND CONCLUSIONS

The behavior of wild white-tailed deer was studied on the 15,000-acre Huntington Forest in the Adirondack Mountains from June, 1963 through February, 1966. Year-round data on distribution and activity were provided by counts of 24-hour accumulations of tracks over 10-and-one-half miles of forest road. Distribution within a wintering area was documented by track and bed counts. Additional data on activity and distribution, and on social behavior and response to disturbance by man were provided by roadside and lakeshore observations of animals, and by spotlighting counts. Marked animals were observed to provide information on social behavior, movements, and ranging. Documentation of vegetation was oriented principally toward evaluating the shelter values of different forest types, and recording changes in cover over the year. Weather measurements were made continuously throughout the study at the base weather station, and periodically in selected study areas. From the standpoint of snow cover, the winter of 1963-64 was slightly more severe than the last ten-year average, while the other two were much less severe than average.

The summary of findings, and the conclusions which follow are restricted to the behavioral aspects of the study, and the discussion of management implications is restricted to that given near the end of Chapters IV, V, and VI.

Deer were found to be generally uniformly distributed over the Forest from May through November, but short-term, local concentrations occurred where food occurred in concentrated abundance. Mineral licks also tended to concentrate deer somewhat from mid-May through July. Distribution from May through October was essentially independent of forest type, physiography, and changes in crown and low-level cover. The trend toward concentration in coniferous shelter types began in November, and during the winter situations with continuous overhead coniferous crown cover, and with west aspects, were favored by deer.

The trend toward concentration of deer in coniferous shelter types was found to be most closely associated with increasing frequency of occurrence of severe windchill (1200 or greater) in November and December. Once concentration was generally established however, distribution was most closely associated with changes in sinking depth of the snow, particularly when sudden reductions in depths over 10 inches occurred through the formation of supporting surface crusts. The trend toward reduced use of coniferous shelter types from mid-March through April was closely associated with decreasing frequency of occurrence of severe windchill.

Within the wintering area studied few differences were found in temperature or relative humidity between forested and exposed locations. Large differences were found in wind however, especially between the exposed lake and all forest stations. Within the forest wind was consistently least in the conifer type. Snow depth was also least in this type but at times the differences between depths in all types were small. The distribution of deer beds within the area was closely correlated with the extent of coniferous crown cover in the different forest types. Of 347 beds tallied in 1964 over 87 percent were in the two types averaging 51 and 63 percent crown cover, over 12 percent in the type averaging 29 percent crown cover, and less than one percent in the type averaging 11 percent cover. In addition, actual bed sites were consistently found where the snow was shallower than the average, even when the deepest snow was relatively shallow. Thus, through their bedding behavior, deer rested in areas of shallow snow and reduced wind. The former is not physically valuable <u>per se</u>, as deeper snow would often serve to better insulate resting animals, but the habit of bedding close to the boles of trees may reduce air movement over the animals. The value of bedding in sheltered areas where less wind occurs - hence windchill is reduced - is doubtless considerable.

The distribution of observations of marked deer indicated that some individuals wintered on a restricted portion of their summer-fall range, while others apparently wintered on ranges that were essentially distinct from their summer-fall ranges. Annual home range estimates for four deer in the adult and yearling classes ranged from 445 to 595 acres, while the estimate for one fawn was 350 acres. Summer-fall home range estimates for 11 deer ranged from 105 to 595 acres, indicating considerable variation. Summer movements also varied considerably with some individuals appearing nearly sedentary, while others sometimes moved one to two miles in less than 24 hours.

Of the 23 marked deer which could be recognized as individuals in 1964, a minimum of 10 (43%) were seen on the area in 1965. Among the age classes the minimum percentages which remained were: (1) adults - 50; (2) yearlings - 29; and (3) fawns - 50. These are known to be minimal figures as some marked deer lost part of their markings and, while still on the area in 1965, could not be identified as individuals. These limited data indicated that there was not a rapid turnover of the population through mortality or emigration, and that the yearling class probably contributes the most of those deer which do emigrate.

A pattern of activity which was positively correlated with hours of daylight was recorded from March through October. A multiple correlation analysis based on 91 track counts indicated that neither maximum daily temperature nor minimum daily relative humidity were significantly correlated with activity when day length was held constant. Seventy-six percent of the variation in activity was attributable to day length, temperature, and humidity combined, while 74 percent could be attributed to day length alone. The strong correlation between activity and day length suggests a well-established pattern with a firm physiological basis, and evidence from other studies indicates the probable relationships. Thus, the activity pattern observed is most likely the result of changes in light acting on the pituitary which controls the production of thyroxin by the thyroid, which in turn regulates metabolism. As basal metabolism and food consumption in captive white-tails has been found to be least in winter and greatest in summer, the March-October activity pattern is probably the result of changing food requirements over the seasons.

Activity was highest in May and June when the deer were moulting and first in their thin summer coats. The daily range of temperatures during these months was consistently greater than in other months, and these variations in temperature acting on relatively poorly insulated animals may have contributed to the high activity observed.

Correlation analyses for late spring and summer activity showed significant negative correlations between activity and day of observation (which is equivalent to positive correlations with day length). This was true for both daytime and nighttime activity. While total activity within a given 24-hour period decreased from June through October, the proportion of the total activity occuring from 6 A.M. to 6 P.M. increased. No explanation for this latter trend was apparent. Activity during the 6 A.M. to 6 P.M. period followed no predictable pattern, and midday activity (10 A.M.-2 P.M.) was not consistently lower than morning or afternoon activity. At the lake daytime activity rose steadily from 9 A.M. through about 11:30 A.M., then remained essentially stable until after 3 P.M. when it began to decline. I conclude that midday heat in this region is not of sufficient duration to depress deer activity.

The only weather factor that was significantly correlated with activity in summer was relative humidity which was negatively related to activity at Deer Lake (this implies a positive correlation with temperature, but none of these correlations were significant). Activity on the lake was greatest on clear and partly cloudy days, intermediate on cloudy days, and lowest on rainy days. Nighttime activity (11 P.M.-1 A.M.) appeared to be more closely correlated with weather measured at 7 P.M. than with weather during the counting period. Deer seen within the 11 P.M. to 1 A.M. period were positively correlated with 7 P.M. temperature, and generally negatively associated with rain occurring during the evening. Rain, lightning, thunder, etc., within the spotlighting period did not affect activity appreciably.

The increased activity from late October through November was closely associated with the rut. This dramatic increase occurred as day length decreased, and daily activity was essentially independent of weather except for storms which depressed activity.

Winter activity was difficult to determine due to changes in distribution. Daily activity in January and February was positively correlated with maximum daily temperature, but not with sinking depth, nor any other weather factor. Daily feed consumption for one penned deer from November through January was also positively correlated with maximum daily temperature. Snowfall usually depressed activity somewhat, and severe snow and ice storms resulted in markedly reduced activity.

No marked relationships were discerned between deer activity and seasonal changes in food and cover, changes in abundance of biting flies, nor changes in human activity.

Several morphological and physiological conditions of the deer were associated with prominent portions of the annual activity pattern. The dramatic increase in activity from April through mid-June coincided closely with the spring moult from the heavy winter to sparse summer coat. The peak of activity in late May and June occurred during the height of the fawning season. The subsequent gradual decrease in activity generally coincided with the nursing period, and the latter part of the decline also coincided with the autumnal moult from summer to winter coats. Finally, the sharp rise in activity from late October through November occurred as rutting activity increased. These observations do not all suggest meaningful correlations, but they do tend to support the multiple correlation analyses and other observations which indicate that activity is not closely correlated with climatic and biotic factors, but rather essentially regulated by underlying physiological processes.

Conclusions on social behavior are difficult to make from the limited information available, and the following comments are subject to cautious interpretation. Groups in summer appeared to be somewhat dynamic in composition, with temporary associations being common. Throughout the summer most adult does were seen alone or with their newborn fawns, while most yearlings were alone or with other yearlings. Some yearlings apparently rejoined the matriarchal group in the fall, as did some adult deer. Adult males associated almost exclusively with other adult bucks, and did so with few manifestations of hostility or aggression. On the lake these males were generally avoided by other deer, and encounters were infrequent. In groups of feeding deer large does were the dominant animals.

Deer use of Deer Lake was found to be closely associated with the abundance, condition, and distribution of aquatic food, particularly water shield. The intensive use of this floating-leaved plant by both wading and swimming deer demonstrates the ability of white-tails to take advantage of a concentrated food supply even under difficult conditions. This same ability to take advantage of food in concentrated abundance was shown by deer in winter when they fed on the tops of trees felled by logging.

Deer were found to respond less violently to disturbance by humans and vehicles in summer, than at other seasons. A broad trend of less pronounced response occurred from March through July, and reversed from July through the winter. While there is doubtless some value in lessened flight response of does with newborn fawns in summer, and in increased response as the traditional fall hunting season approaches, the significance of the overall pattern is not clear.

A synthesis of the most significant of the foregoing results and conclusions is a difficult, but challenging task. The following paragraphs are offered as a brief attempt toward this end.

The activity patterns documented in this study seem to me to indicate that the white-tailed deer has evolved an extremely valuable physiological adaptation which fits it well for its harsh environment in these latitudes. Apparently metabolism and consequent food requirements are high when food supplies are relatively abundant, and activity levels follow as the tangible manifestation of these phenomena. In winter, when food supplies are restricted, metabolism is apparently lowered, and activity is lessened accordingly. These changes apparently occur in response to changes in day length, not temperature, although activity is positively correlated with temperature in some seasons.

The ability of the deer to exploit concentrated supplies of food in both summer and winter demonstrates that the behavior of the species is adaptable - that is readily modified to take advantage of changes in the environment. A striking example of this is that of swimming deer, which, while structurally poorly equipped for swimming (or even wading on soft bottoms), can still avail themselves of an abundant supply of aquatic food. I believe that the same holds for winter behavior, but the case is perhaps less clear than in summer. The ability of the white-tail to utilize local shelter situations rather than to expose itself to the hazards of actual migration is further evidence of the adaptability of the deer. Some, however, question this, because the deer supposedly seeks shelter in food deficient areas when "adequate" supplies of food are nearby. I believe that this question is one of degree rather than kind. How much food in winter is adequate where shelter from windchill may be deficient? How much food is actually required if metabolism is lowered in the worst part of the winter? What are the required balances between consumption of food and ambient temperature and windchill regimens under different weather conditions? Most important, what part of the entire range offers the most promise for survival of an adequate breeding population under the most severe climatic conditions which may occur? These are the questions which I believe really pertain to the evaluation of the winter behavior of deer. That some animals succumb to malnutrition in winter is hardly evidence enough to conclude that deer do not behave intelligently then. That many survive to reproduce and thereby perpetuate the species seems to me to be the more telling fact on the question of the behavior of white-tails in winter.

In short, I believe that the results of this study clearly amplify the conclusions of others on captive deer which indicate that the white-tail is physiologically well-adapted for life in a rigorous environment. Within this frame of reference, the ability of the deer to take advantage of concentrations of food and shelter demonstrates its adaptability. Thus, not only is the white-tailed deer one of the most beautiful and valuable animals in North America, it must also be one of the best adapted and most adaptable.

Prepared by:

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Table 1. Comparison of percent occurrence of selected environmental factors along four 210-chain divisions of forest road[1].

Environmental Factor	Road Division[2] Adjidaumo 0-205	Adjidaumo 210-Wolf Lake 135	Wolf Lake 140-Catlin Lake 210	Catlin Lake 0-205
Forest Shelter Type[3]				
No Conifers	28	48	17	33
Scattered Conifers	31	40	31	19
Islands Of Conifers	40	12	14	43
Continous Conifers	0	0	38	5
Aspect				
North	10	38	26	0
East	10	45	0	24
South	31	12	0	26
West	43	0	71	43
Flat	7	5	2	7
Other				
Meadows	48	0	2	0
Clearings	57	38	54	26
Lakeshores	28	19	57	21

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[1] Based on occurrence of factors in 5-chain sections.

[2] The locations of these divisions of road are shown in Figure 1.

[3] S.A.F. types 25, 25, transition from 25 to 24 or 32, and 24 or 32 respectively.

Table 2. Monthly mean track count scores for four 210-chain divisions of forest road, September, 1963-February, 1966.[1]

		Road Division[2]			
Month	Number Of Counts	Adjidaumo 0-205	Adjidaumo 210-Wolf Lake 135	Wolf Lake 140-Catlin Lake 210	Catlin Lake 0-205
January	10	8.6	13.4	17.6	10.7
February	10	5.9	12.9	24.2	11.8
March	8	1.9	3.6	22.0	11.5
April	4	9.5	5.2	12.5	14.5
May	5	28.6	20.8	26.6	32.2
June	4	36.2	35.5	32.2	30.0
July	1	29.0	28.0	18.0	15.0
August	2	13.0	17.0	10.5	14.5
September	10	13.4	11.4	11.4	10.3
October	9	9.3	13.1	11.6	12.0
November	7	22.0	21.8	18.4	19.1
December	5	6.6	13.0	19.2	18.0

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[1] Based on the number of 5-chain sections with tracks in 24 hours.

[2] The locations of these divisions of road are shown in Figure 1.

Table 3. Number of deer observed each month along five 210-chain divisions of forest road, June, 1963-December, 1965.

Month	Number[1] Of Trips	Road Division[2]					
		Adjidaumo 0-205	Adjidaumo 210-Wolf Lake 135	Wolf Lake 140-Catlin Lake 210	Catlin Lake 0-205	Shattuck Clearing 0-205	Total
January	24	2	3	14	3	2	24
February	22	3	0	17	13	3	36
March	32	10	1	14	5	15	45
April	22	20	0	4	14	16	54
May	86	38	4	10	24	22	98
June	591	308	35	112	130	174	759
July	584	369	25	76	166	179	815
August	359	260	34	41	85	181	601
September	178	38	9	11	24	28	110
October	148	73	6	15	28	39	161
November	108	41	8	27	12	34	122
December	12	2	1	2	1	1	7
Total	2166	1164	126	343	505	694	2832

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[1] All trips do not include all divisions of road, hence, the number of trips may only be related to the total numbers of deer observed

[2] The locations of these divisions of road are shown in Figure 1.

Table 4. Numbers of deer observed at different locations on spotlighting counts, May-August, 1965.

Period	Number Of Nights	Location			Total
		Highway[1]	Salt Lick	Other	
May 17-31	11	35	40	15	90
June 1-15	9	15	33	28	76
June 16-30	7	3	35	25	63
July 1-15	4	0	14	6	20
July 16-31	8	3	21	15	39
August 1-15	6	5	2	9	16
August 16-31	3	0	0	6	6
Total	48	61	145	104	310

[1] The highway area offers green herbage before other areas in the spring, and appears to provide some salt attractant on the gravel shoulders and in adjacent low, wet areas.

Table 5. Deer use index levels for shelter type-aspect combinations as indicated by track counts over ten-and-one-half miles of forest road, December-March, 1963-1966.[1]

	Shelter Type			
Aspect	No Conifers	Scattered Conifers	Islands Of Conifers	Continuous Conifers
North	0.94	1.14	0.57*	1.56*
East	0.47	0.95	0.86*	0.35*
South	0.51	0.74	1.07	-
West	1.05	1.22	1.25	1.66
Flat	1.08*	0.70*	0.62	-

[1] Deer use index equals the percent of the total track score which occurred in each type-aspect combination divided by the percent frequency occurrence of the combination. An index of 1.00 indicates deer use as expected on the basis of occurrence of the combination alone. The total track score for the period was 2135.

* Frequency of occurrence of type-aspect combination less than 2 percent.

Table 6. Selected monthly temperature statistics for the base weather station, 1963-1965.

Month	Degree Days[1]			Mean Maximum minus Mean Minimum			Number Of Days With Minimum 0°F. or Below		
	1963	1964	1965	1963	1964	1965	1963	1964	1965
January	1535	1400	1571	14.1	16.0	17.8	10	7	9
February	1479	1416	1328	19.1	20.0	18.0	13	10	10
March	1153	1123	1220	18.2	18.0	18.2	1	0	3
April	792	746	857	20.1	21.9	19.7	0	1	1
May	379	214	333	25.3	28.0	28.6	0	0	0
June	101	124	189	25.7	25.1	25.2	0	0	0
July	55	12	113	22.4	21.0	22.9	0	0	0
August	153	120	135	19.2	20.8	18.7	0	0	0
September	398	233	256	25.4	22.9	17.5	0	0	0
October	479	-	679	26.3	19.5	15.1	0	0	0
November	806	845	-	10.4	14.2	11.3	0	0	0
December	1623	1311	1229	14.6	14.5	10.3	10	4	2

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[1] Monthly degree days are the sums of the negative departures of average daily temperatures from 65°F.

Table 7. Selected monthly relative humidity statistics for the base weather station, 1963-1965.[1]

	1963			1964			1965		
Month	Mean Maximum	Mean Minimum	Mean Max. Minus Mean Min.	Mean Maximum	Mean Minimum	Mean Max. Minus Mean Min.	Mean Maximum	Mean Minimum	Mean Max. Minus Mean Min.
January	85	82	3	97	73	24	94	68	26
February	94	71	23	94	58	36	94	64	30
March	97	62	35	95	56	39	97	56	41
April	96	51	45	95	50	45	96	51	45
May	99	45	54	98	41	57	100	39	61
June	100	50	50	99	46	53	100	47	53
July	100	51	49	100	56	44	100	49	51
August	100	57	43	100	54	46	100	62	38
September	100	41	59	100	53	47	100	69	31
October	99	41	58	100	55	45	99	70	29
November	99	77	22	100	68	32	98	83	15
December	94	80	14	99	87	12	99	89	10

[1] All figures are percent relative humidity.

Table 8. Inches of precipitation per month at the base weather station, 1963-1965.

Month	Year 1963	 1964	 1965	Total
January	2.17	4.05	2.28	8.50
February	2.06	0.97	3.32	6.35
March	4.17	4.41	1.59	10.17
April	2.74	2.72	2.86	8.32
May	2.82	3.82	0.34	6.98
June	2.59	1.91	2.09	6.59
July	1.83	3.93	2.01	7.77
August	3.93	3.92	7.52	15.37
September	1.28	0.78	3.10	5.16
October	0.28	1.31	3.22	4.81
November	3.93	2.69	4.69	11.31
December	1.85	2.89	1.68	6.42
Total	29.65	33.40	34.70	97.75

Table 9. **Number of days per month with a minimum of 10, 15, and 20 inches of snow cover at the base weather station, December-April, 1956-1966.**

	Month																	
	December			January			February			March			April			Total		
Winter	10	15	20	10	15	20	10	15	20	10	15	20	10	15	20	10	15	20
1956-57	8	0	0	23	10	0	0	0	0	3	0	0	0	0	0	34	10	0
1957-58	0	0	0	17	8	0	28	28	21	31	29	24	2	0	0	78	65	45
1958-59	31	29	6	31	31	22	28	28	28	31	31	31	12	9	7	133	128	94
1959-60	14	3	2	31	31	29	29	29	29	31	31	31	13	12	11	118	106	102
1960-61	5	0	0	31	31	0	24	19	0	22	6	0	6	2	0	88	58	0
1961-62	4	0	0	31	3	0	28	23	15	31	31	29	9	5	0	103	62	44
1962-63	10	0	0	31	8	5	28	28	28	31	31	31	12	5	0	112	72	64
1963-64	10	0	0	31	29	1	29	29	27	31	29	12	12	11	4	113	98	44
1964-65	0	0	0	10	5	0	28	17	1	31	11	1	9	4	0	78	37	2
1965-66	0	0	0	9	2	1	28	21	5	31	15	0	9	0	0	77	38	6
Mean	8.2	3.2	0.8	24.5	15.8	5.8	25.0	22.2	15.4	27.3	21.4	15.9	8.4	4.8	2.2	93.4	67.4	40.1

Table 10. Selected monthly wind statistics for the base weather station, October, 1964–December, 1965.

Month	Hours Recorded	Percent Of Hours With Wind 2 MPH Or Greater	Percent Of Hours With Gusts 10 MPH Or Greater	Mean Maximum (mph)
October	672	54	20	18
November	720	57	25	13
December	744	41	13	13
January	744	58	27	17
February	672	62	36	19
March	744	53	22	16
April	672	56	21	15
May	744	59	24	19
June	720	56	22	18
July	744	54	16	15
August	744	45	12	13
September	720	45	6	10
October	744	59	24	17
November	720	60	22	15
December	712	62	7	10

Table 11. Number of hours of selected levels of windchill occurring semi-monthly at the base weather station, November, 1964 through April, 1965.

Period	Windchill Equal To Or Greater Than			
	800	1000	1200	1400
November 1-15	51	10	0	0
November 16-30[1]	144	57	10	0
December 1-15	104	51	35	21
December 16-31	119	57	23	9
January 1-15	177	132	73	38
January 16-31	214	165	61	8
February 1-15	151	93	38	3
February 16-28	210	178	108	71
March 1-15	120	68	29	2
March 16-31	169	98	52	2
April 1-15[2]	91	34	6	0
April 16-30	45	3	0	0

1 November 16 and 17 not included

2 April 9-12 not included

Table 12. Descriptive statistics for the major forest types in the Deer Creek wintering area.

Statistic	Forest Type[1] Hardwood	Hardwood-Conifer	Conifer-Hardwood	Conifer
Number Of Stations	10	35	66	56
Percent Frequency	6	21	39	34
Mean Percent Coniferous Crown Cover	11.3	29.3	50.8	62.8
95% Confidence Interval, Coniferous Crown Cover	8.1-14.5	22.7-35.9	44.5-57.1	57.3-68.3
Mean Basal Area, Conifers, Square Feet Per Acre	5.0	19.7	51.4	62.4
95% Confidence Interval, Basal Area, Conifers	0.0-10.1	15.4-24.6	43.2-58.6	55.1-69.7
Mean Basal Area, Total, Square Feet Per Acre	138	105	118	121

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[1] From left to right - S.A.F. types 25, 25 or transitions between 25 and 24 or 32, transitions between 25 and 24 or 32, and 24 or 32 respectively.

Table 13. Description of the locations of weather stations in the Deer Creek wintering area.

Station	Habitat Type	Coniferous Crown Cover (percent)	Elevation (feet)	Aspect	Slope
28	Hardwood	0	1790	South	Moderate
49	Conifer-Hardwood	44	1700	South	Moderate
117	Conifer	74	1650	South-west	Slight
157	Hardwood-Conifer	28	1760	South	Moderate
BP	Exposed Lake	0	1600	Flat	None

Table 14. Comparison of average miles of wind per day in four forest types in the Deer Creek wintering area, and on an exposed lake, February 18-April 12, 1965.[1]

	Habitat Type				
Period	Hardwood	Hardwood-Conifer	Conifer-Hardwood	Conifer	Lake
February 18-23	21.3	22.2	27.1	18.6	208.3
February 23-March 1	46.4	36.7	35.0	22.0	212.0
March 1-8	25.3	16.2	14.8	7.5	103.6
March 8-15	14.0	13.9	17.3	11.2	118.7
March 15-22	24.9	20.1	23.0	12.0	132.4
March 22-29	27.1	17.8	20.9	11.4	139.8
March 29-April 5	21.9	17.6	23.6	18.1	135.7
April 5-12	26.9	17.3	21.5	9.2	133.5
Overall Average	26.2	20.2	21.6	13.8	148.0

[1] Wind measured by totalizing anemometers positioned approximately three feet above the surface of the snow.

Table 15. Results of analyses of variance of snow depths in four forest types in the Deer Creek wintering area, January 20 and 25, 1965.

Date	Source Of Variation	Sum Of Squares	Degrees Of Freedom	Mean Square	F
January 20	Between Types	30	3	10.00	3.40*
	Within Types	150	51	2.94	-
	Total	180	54	-	-

Snowdepth Means (Inches)
Hardwood - 8.2 Hardwood-Conifer - 8.1 Conifer-Hardwood-7.3
Conifer - 6.3

- -

January 25	Between Types	45	3	15.00	2.94*
	Within Types	260	51	5.10	-
	Total	305	54	-	-

Snowdepth Means (Inches)
Hardwood - 13.8 Hardwood-Conifer - 13.1 Conifer-Hardwood-12.6
Conifer - 11.2

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* Probability of a larger F less than .05.

Table 16. Comparison of average miles of wind per day in three forest types in the Deer Creek wintering area, and on an exposed lake, January 24–February 28, 1966.[1]

	Habitat Type			
Period	Hardwood	Conifer-Hardwood	Conifer	Lake
January 24–February 1	11.6	21.8	-	134.9
February 1-7	7.9	8.8	5.1	46.2
February 7-14	26.8	31.4	18.5	143.4
February 14–22	20.6	35.5	20.2	174.9
February 22–28	11.7	12.2	9.6	78.7
Overall Average	16.2	22.9	14.1	121.0

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[1] Wind measured by totalizing anemometers positioned approximately three feet above the surface of the snow.

Table 17. Distribution of deer beds by forest types and sinking depths in the Deer Creek wintering area, January-March 1964.

		Forest Type			
Period	Sinking[1] Depth (inches)	Hardwood	Hardwood-Conifer	Conifer-Hardwood	Conifer
January					
2-4	13	0	1	6	10
14-16	14	0	7	8	35
28-30	3	0	5	17	22
February					
14-15	7	0	17	44	30
25-26	8	1	10	42	31
March					
12	9	0	3	40	18
Total	-	1	43	157	146

---

[1] Sinking depth - the depth to which a deer will sink under a given snow depth and character - is the average of measurements at 17 stations.

Table 18. Estimated home ranges of 12 marked deer based on observations from March, 1964 through November, 1965.

Name[1]	Age	Number Of Observations	Home Range (acres)[2]	
			Annual	Summer-Fall
Jezabel	Adult	36	445	205
Rasmunda[3]	Adult	42	595	595
Cry-baby[3]	Fawn	24	350	350
Number One[4]	Adult	13	540	540
Tommy[5]	Adult	67	-	sedentary?
Anna-K	Yearling-Adult	113	-	350
Matilda	Adult	26	-	155
Mama[6]	Adult	29	-	215
Lola	Yearling-Adult	44	-	195
Hades	Fawn-Yearling	36	-	255
P-G	Yearling	17	-	105
Oscar[7]	Yearling	56	475	475

---

[1] All females except Oscar.

[2] Based on the area enclosed by polygons formed by connecting the outermost points of observation.

[3] Mother and daughter.

[4] Belled

[5] All 67 observations in a restricted area.

[6] Two observations in 1964, and 24 in 1965; indicating a change in range or behavior, or both.

[7] Killed as a two-and-one-half year old approximately **eight miles** from annual home range of 1964.

Table 19. Number and percent of marked deer of different sexes and ages observed in 1964 which were seen in the summer and fall of 1965.

Sex-Age Class	Number Marked In 1964	Number Positively Observed On Area, Summer-Fall, 1965	Minimum Percent[1] In Area, 1965
Female-Adult	9	4	44
Female-Yearling	6	2	33
Female-Fawn	5	3	60
Male-Adult[2]	1	1	100
Male-Yearling[3]	1	0	0
Male-Fawn	1	0	0
All Adults	10	5	50
All Yearling	7	2	29
All Fawns	6	3	50
All Deer	23	10	43

[1] Known to be minimal as some deer lost part of their markings and could not be identified as individuals.

[2] Sighted on property adjacent to the Huntington Forest in the fall of 1965.

[3] Killed in November, 1965 approximately five miles from 1964 range.

Table 20. Simple, partial, and multiple correlation coefficients for 24-hour track count scores[1] with hours of daylight, maximum temperature, and minimum relative humidity, March-October, 1963-1965 (54 days).

Variable	Simple Correlation Coefficient	Partial Correlation Coefficient	Multiple Correlation Coefficient (R)	R^2
Hours of Daylight	0.86**	0.81**	-	-
Max Temperature °F.	0.61**	0.00	-	-
Min Relative Humidity %	-0.43**	-0.13	-	-
All Combined	-	-	0.87**	0.76

[1] Equivalent to number of 5-chain road sections with tracks.

** t-test or F test for 0 population correlation significant at P = .01; hence these coefficients may be considered as significantly different from 0.

Table 21. Simple, partial, and multiple correlation coefficients for number of deer seen on spot lighting counts with day of observation, temperature, and wind, May through August, 1965 (24 nights).[1]

Variable	Simple Correlation Coefficient	Partial Correlation Coefficient	Multiple Correlation Coefficient (R)	R^2
Day of Observation	-0.80**	-0.91**	-	-
Mean Temperature - °F.	-0.06	0.28	-	-
Mean Wind - mph	0.32	0.10	-	-
All Combined	-	-	0.86*	0.74

[1] Selected for relative humidity at or near saturation, i.e., 90-100 percent.

* t-test or F test for 0 population correlation significant at P = .05; ** at P = .01; hence these coefficients may be considered a significantly different from 0.

Table 22. Simple, partial, and multiple correlation coefficients for number deer seen on spot lighting counts with day of observation, temperature, relative humidity, and wind measured four hours prior to spot lighting, May-August, 1965 (36 nights)[1]

Variable	Simple Correlation Coefficient	Partial Correlation Coefficient	Multiple Correlation Coefficient (R)	R^2
Day of Observation	-0.70**	-0.95**	-	-
Temperature °F.	0.06	0.46**	-	-
Relative Humidity %	-0.18	-0.13	-	-
Wind mph	0.28	-0.10	-	-
All Combined	-	-	0.83*	0.69

---

[1] This approach was required to include a variety of relative humidity scores, as humidity was always high during the spot lighting period.

* t-test or F test for 0 population correlation significant at P = .05; ** at P = .01; hence these coefficients may be considered as significantly differnnt from 0.

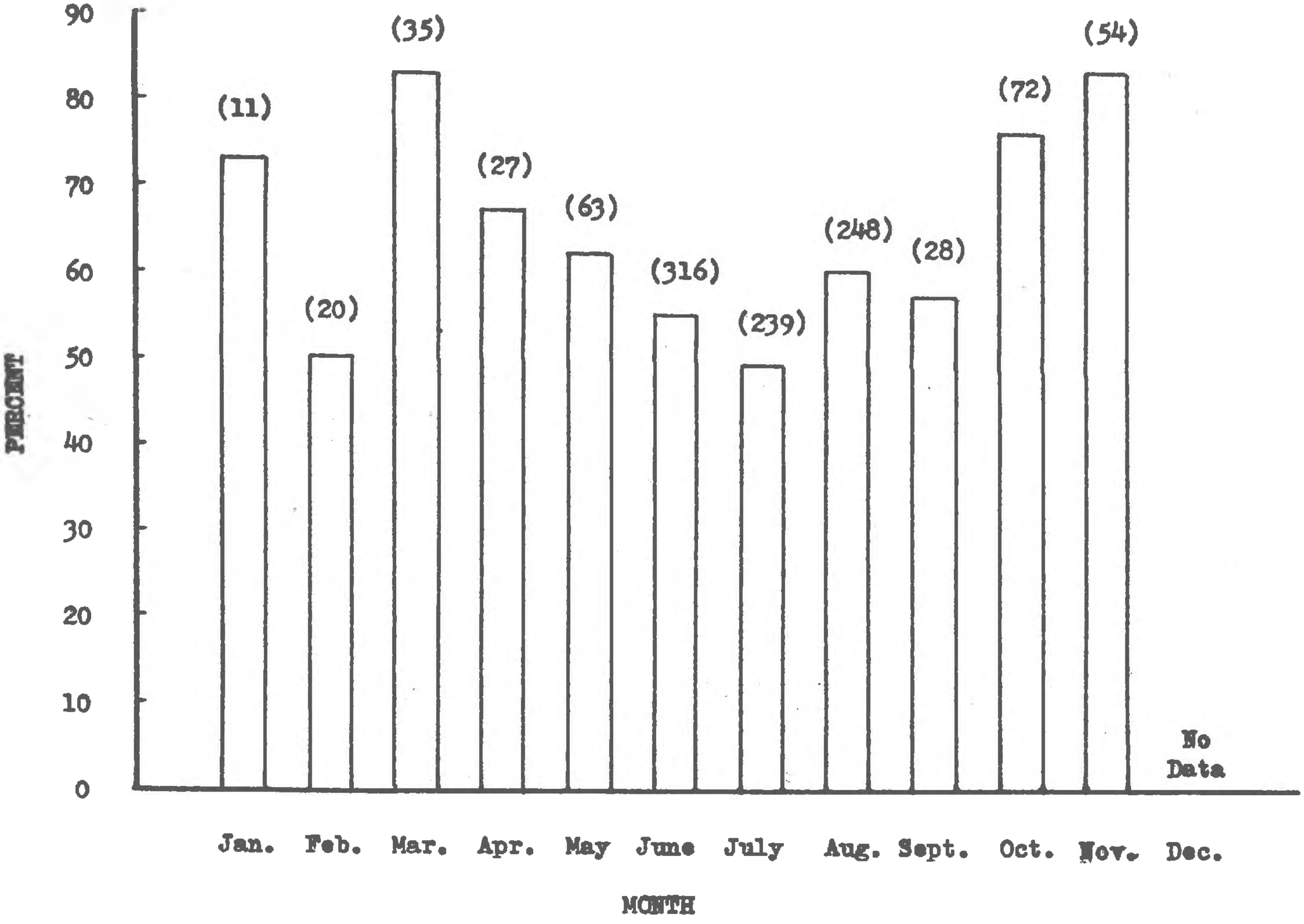

Figure 15. Monthly percentages of deer fleeing the roadside with their tails up. (The figures over each bar indicate the total number of deer recorded fleeing with their tails either distinctly up or down)

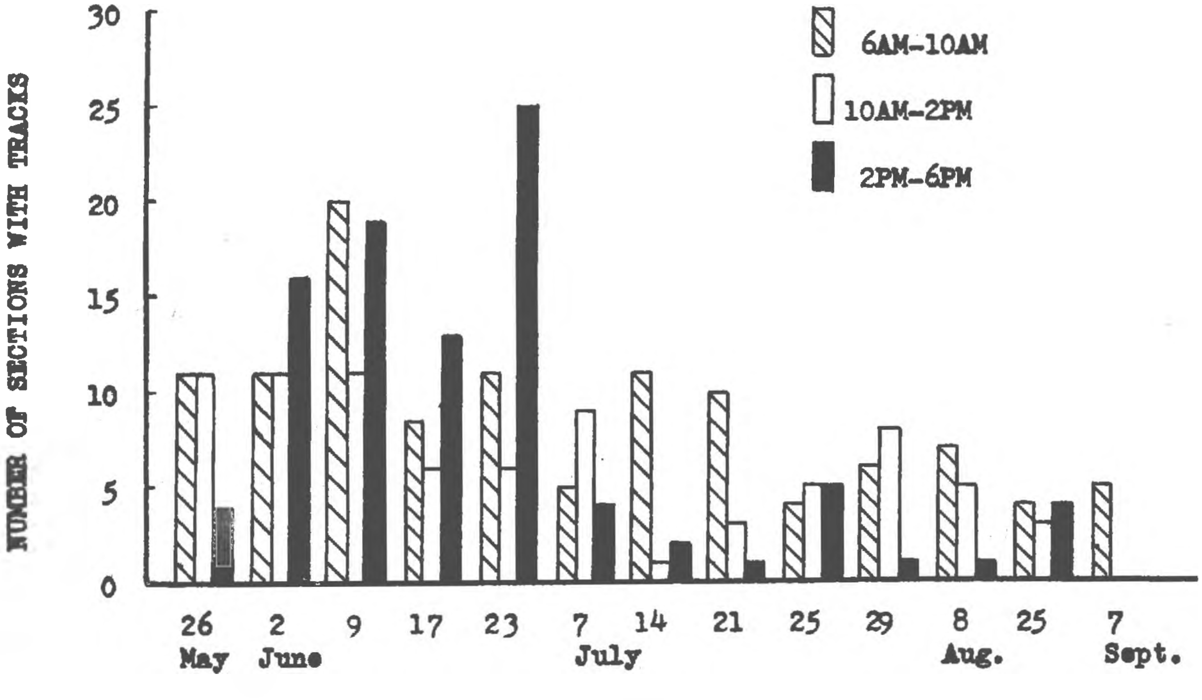

Figure 10. Comparison of deer activity during daylight hours as indicated by four-hour track accumulations over two-and-three-tenths miles of forest road, May-September, 1965.

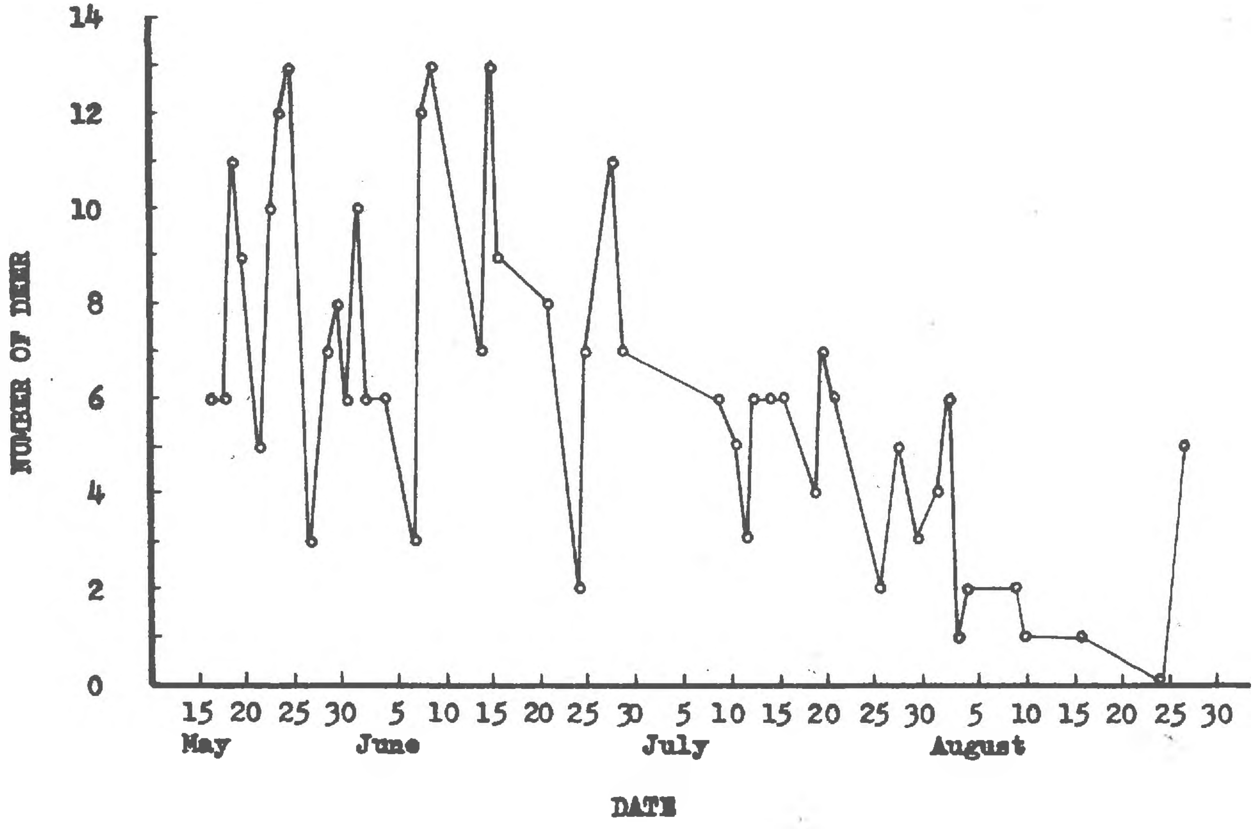

Figure 9. Numbers of deer recorded on spotlighting counts, May-August, 1965.

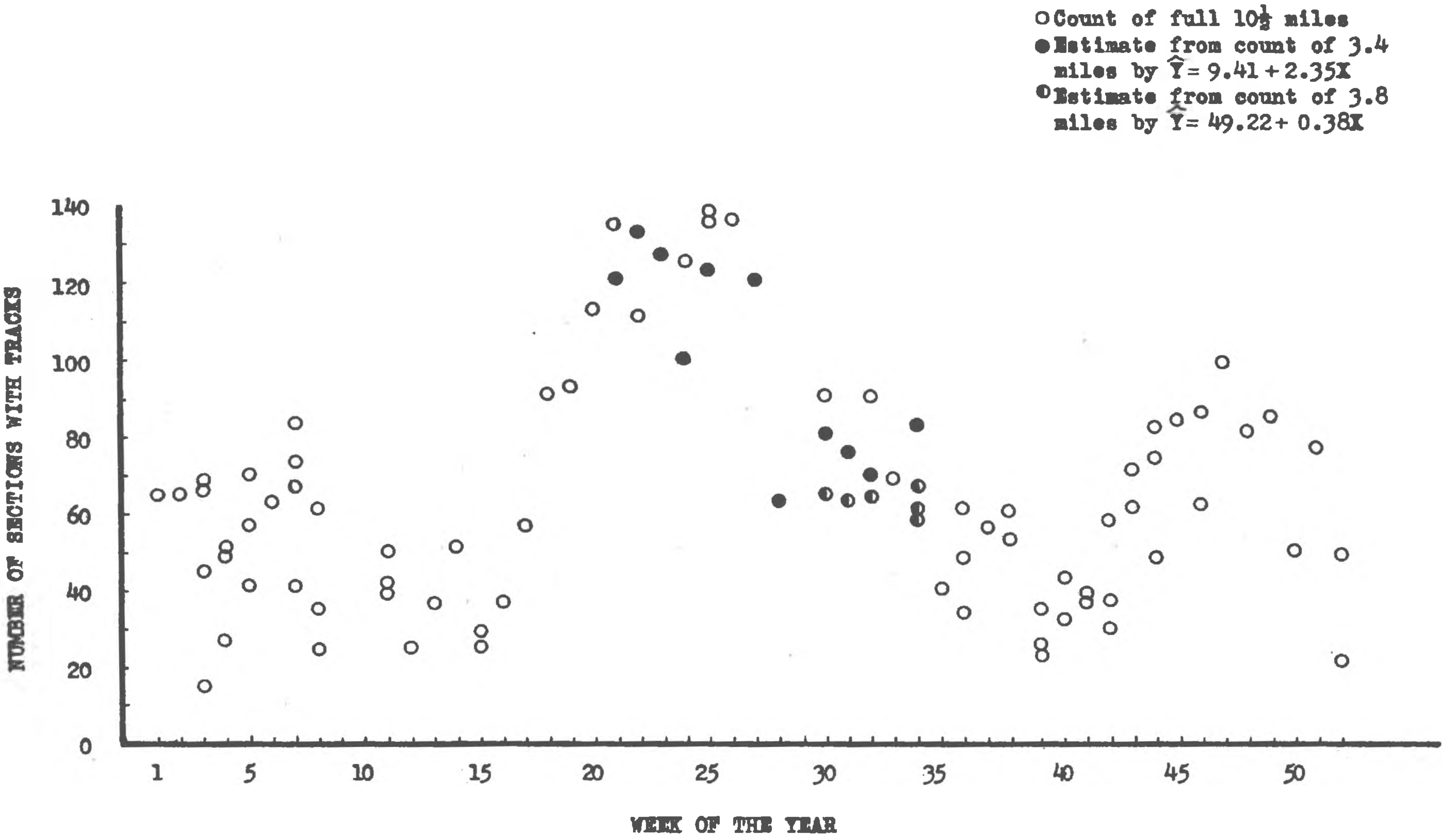

Figure 8. Weekly activity levels of deer as indicated by 24-hour track accumulations, July, 1963-February, 1966.

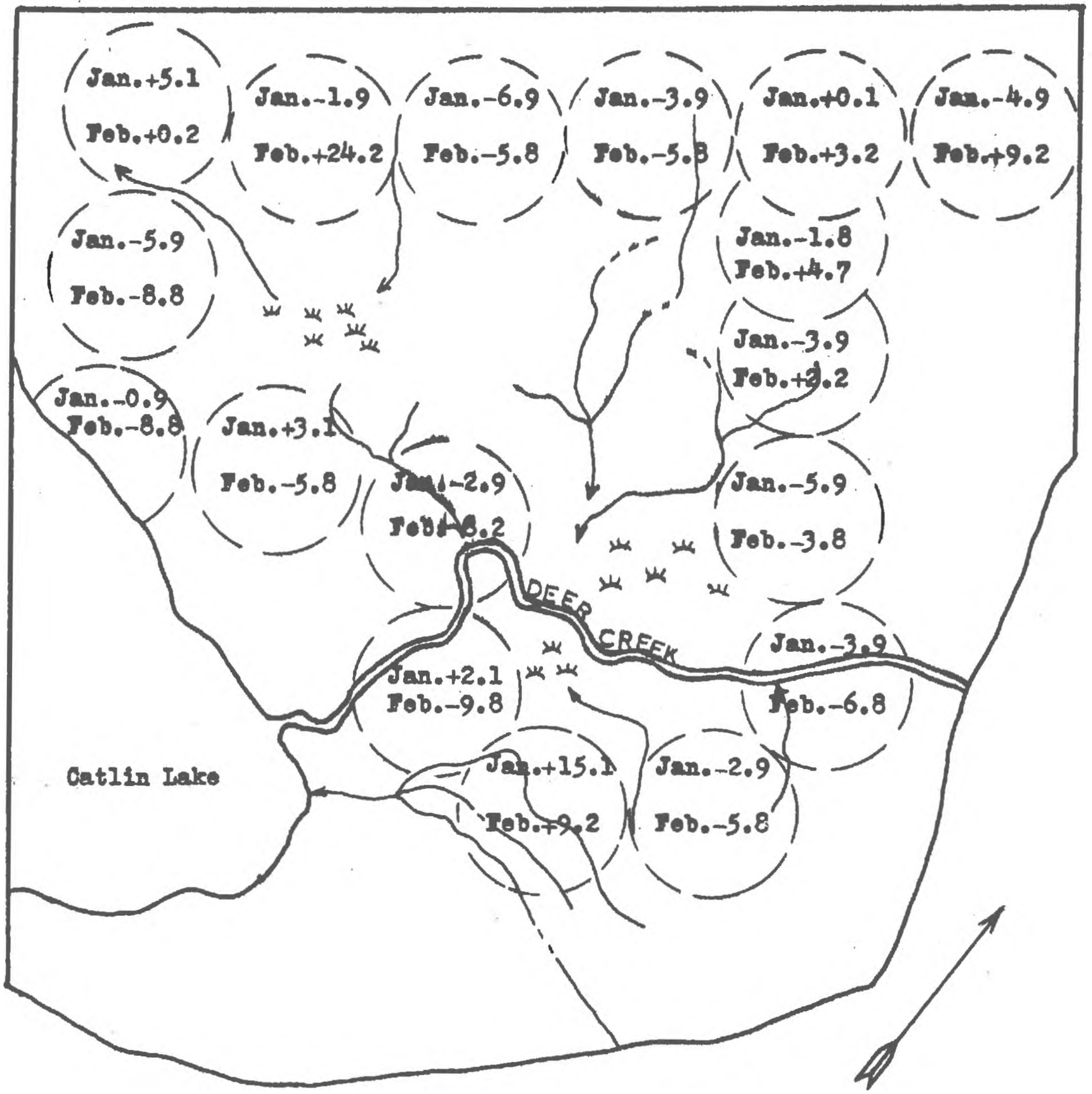

Figure 7. Distribution of deer bedding in the Deer Creek wintering area in January and February, 1964, as indicated by deviations from the expected number of beds for sub-sample sections. (The signed figures are the deviations from the number of beds expected on the basis of proportionate distribution of the total number of beds recorded for each month)

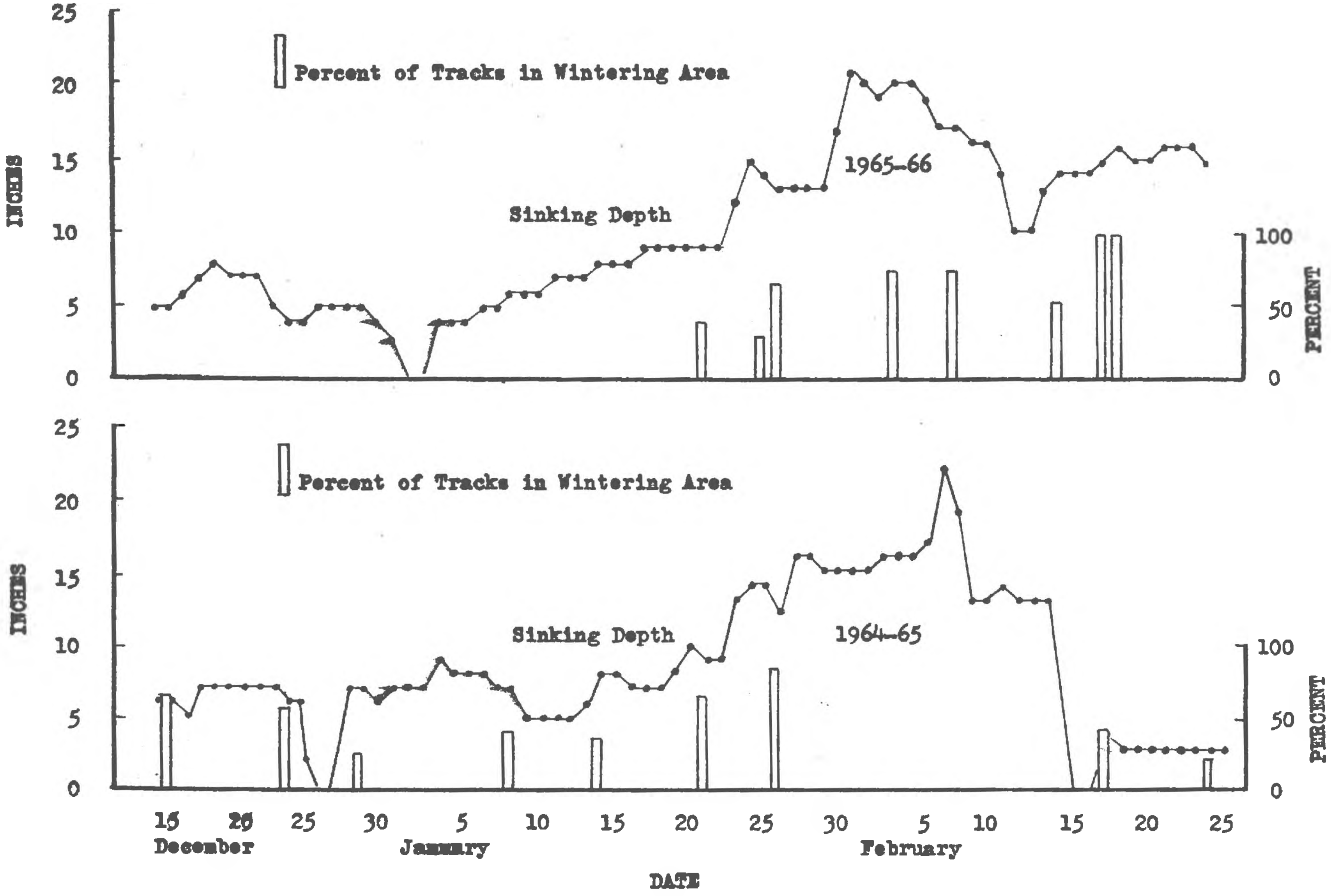

Figure 6. Trends in deer use of a wintering area and in sinking depth for two winters.

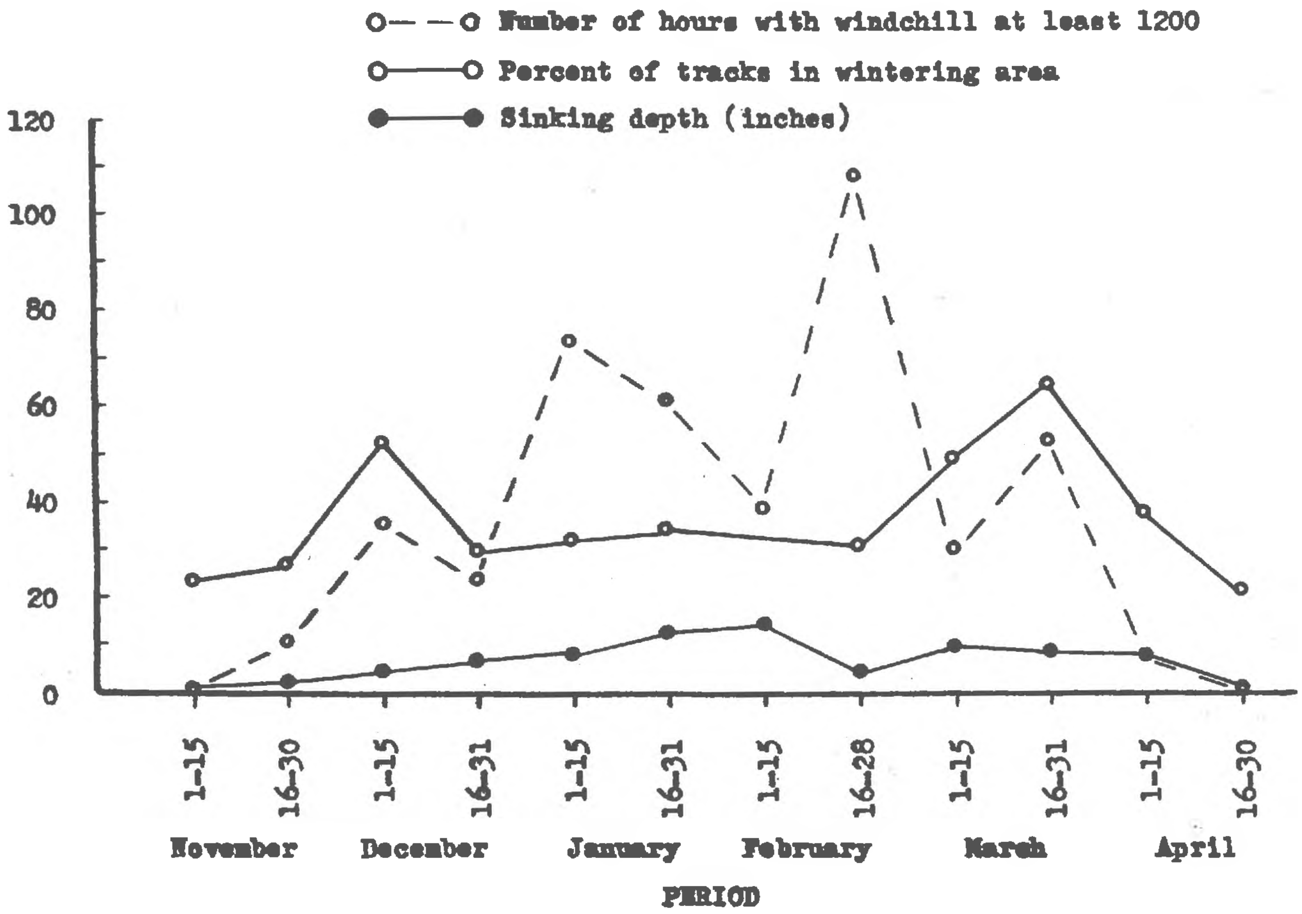

Figure 5. Trends in deer use of a wintering area compared to trends in windchill and sinking depth, November, 1964-April, 1965.

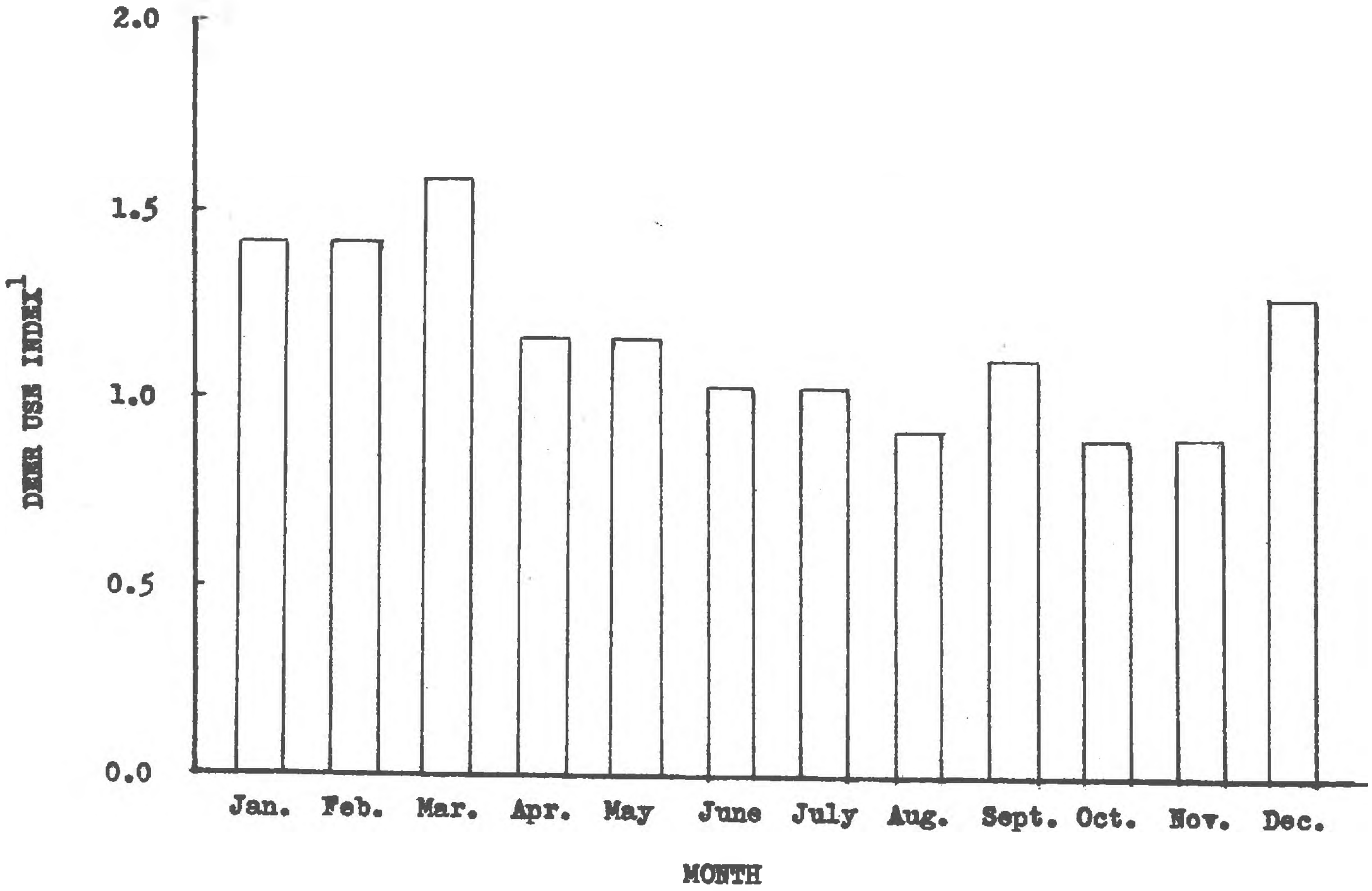

Figure.4. Monthly deer use index levels for the west aspect as indicated by 75 trackcounts over ten-and-one-half miles of forest road, September, 1963-February, 1966.

[1] Equals the percent of the total track score which occurred on this aspect divided by the percent frequency of occurrence of the aspect. An index of 1.0 indicates deer use as expected on the basis of occurrence of the aspect alone.

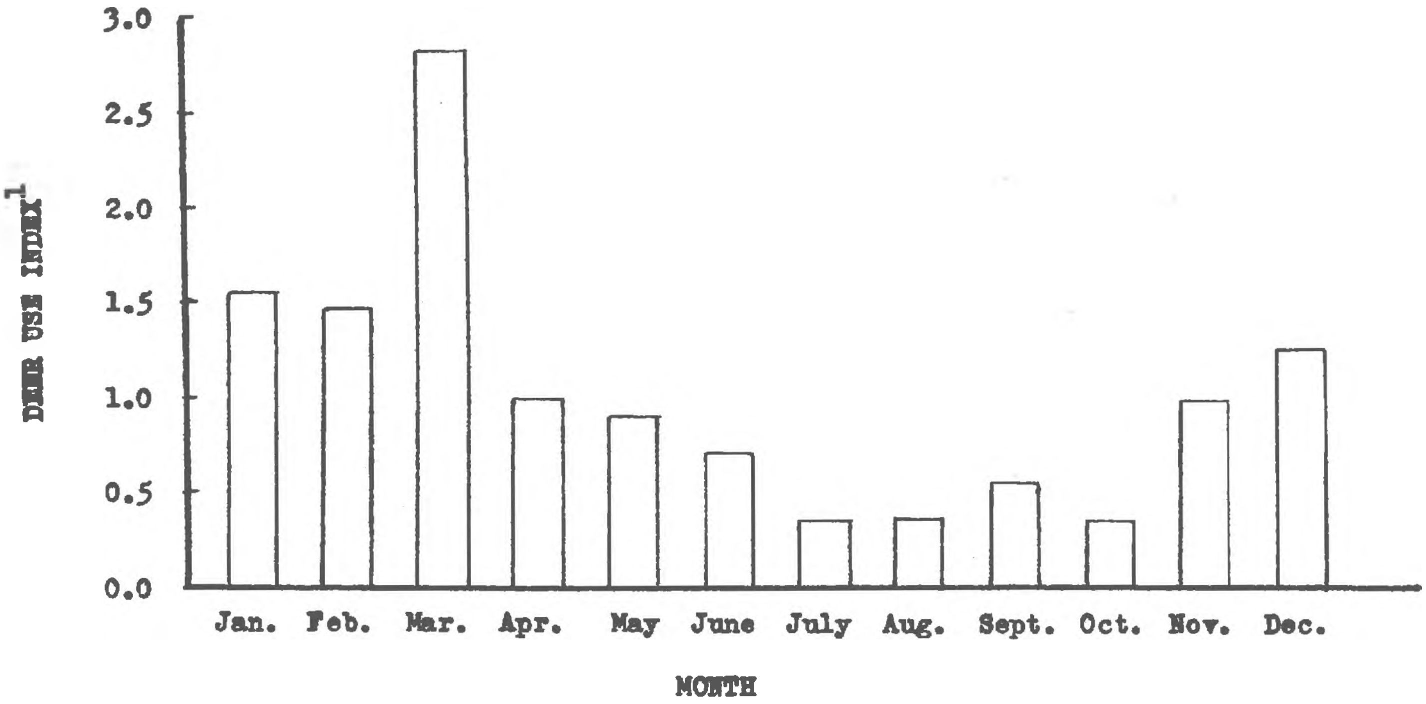

Figure 3. Monthly deer use index levels for the continuous conifers shelter type as indicated by 75 track counts over ten-and-one-half miles of forest road, September, 1963–February, 1966.

[1] Equals the percent of the total track score which occurred in this shelter type divided by the percent frequency of occurrence of the type. An index of 1.0 indicates deer use as expected on the basis of occurrence of the type alone.

Figure 2 -- Large Cover Map of the Huntington Forest. (Not included in the printed copies because of size).

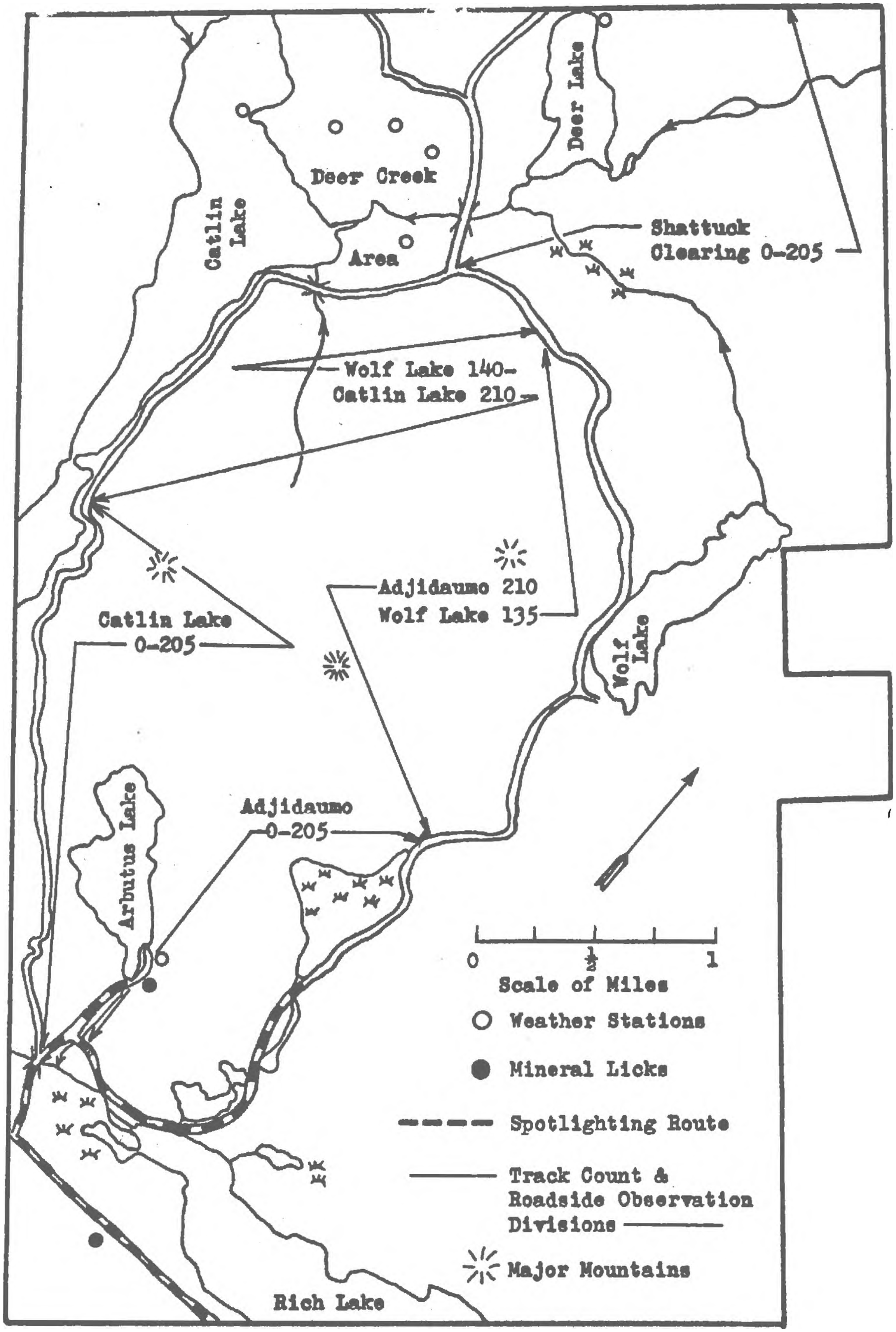

Figure 1. Abbreviated map of the Huntington Forest showing the principal study areas.

Table 26. Monthly percentages of roadside observations of deer by selected sex and age combinations, June, 1963 – February, 1966.

Month	Number Of Observations	Sex And Age Combination[1]								
		F	F&F	F&Fa	F&M	M	M&M	Fa	Fa&Fa	M&Fa
January	11	36.4	63.6	–	–	–	–	–	–	–
February	17	35.2	64.8	–	–	–	–	–	–	–
March	21	19.0	81.0	–	–	–	–	–	–	–
April	12	25.0	75.0	–	–	–	–	–	–	–
May	46	50.0	21.7	10.8	6.5	6.5	–	4.3	–	–
June	482	63.9	8.5	10.3	2.6	11.8	1.4	1.0	0.2	–
July	600	56.8	10.0	11.0	1.3	16.0	1.7	1.7	0.8	0.7
August	439	49.9	14.4	15.5	1.1	10.7	1.8	3.9	2.5	0.2
September	85	44.7	17.6	10.6	7.0	5.9	–	8.2	4.7	1.2
October	91	39.6	31.9	14.3	5.5	6.5	1.1	1.1	–	–
November	72	29.2	22.2	12.5	5.6	27.7	–	1.4	1.4	–
December	4	. . . . insufficient data								
Total	1880	53.5	14.8	11.7	2.3	12.4	1.4	2.3	1.2	0.3

[1] Abbreviations are: F–female; M–male; Fa–fawn. January–April observations include some unrecognizable males. Some unrecognizable immature males may be included in other months.

Table 25. Monthly percentages of roadside observations of deer by number per observation, June, 1963–February, 1966.

Month	Number Of Observations	Number Of Deer Per Observation One	Two	Three	Four–Six
January	12	41.7	41.7	–	16.6
February	30	36.7	30.0	16.6	16.6
March	26	34.6	34.6	15.4	15.4
April	24	25.0	41.7	12.5	20.8
May	61	57.4	32.8	8.2	1.6
June	628	82.2	14.5	3.0	0.4
July	594	81.8	13.1	4.0	1.0
August	444	63.1	24.5	10.1	2.3
September	82	61.0	28.0	9.8	1.2
October	97	52.6	25.8	16.5	5.2
November	72	56.9	22.2	15.3	5.6
December	4	– – – insufficient data – – –			
Total	2074	72.0	19.1	6.7	2.2

Table 28. Density of water shield on the surface of Deer Lake in June and August, 1964.

Sample Bed Number	June Sample Size	June Mean Density[1]	June Confidence Interval (95%)	August Sample Size	August Mean Density	August Confidence Interval (95%)
1	10	8.7	6.4 - 11.0	10	47.4	30.4 - 64.4
2	10	11.5	6.3 - 16.7	9	40.9	34.0 - 47.8
3	10	17.2	11.5 - 22.9	10	109.0	97.3 -120.7
4	10	8.1	3.1 - 13.1	10	61.7	40.9 - 82.5
5	10	14.5	9.1 - 19.9	10	71.3	47.7 - 94.8
6	10	9.4	5.9 - 12.9	10	66.3	39.7 - 92.9
Total	60	11.6	9.8 - 13.3	59	66.5	57.7 - 75.3

[1] Density based on number of floating leaves per 6.1 square foot sampling hoop. Density per square foot equals tables figures divided by 6.1.

Table 27. Observations of 15 marked deer seen alone and with combinations of other deer, June, 1964–December, 1965.

			Number Of Times Observed				
Name[1]	Year	Age[2]	Alone	With Fawns	With Females	With Males(Y)	With Males(A)
Jezabel	1964	A	19	2	1	0	1
	1965	A	13	0	3	0	1
Number One	1964	A	4	0	1	0	0
	1965	A	3	0	1	0	1
Mama	1964	A	2	0	0	0	0
	1965	A	22	4	1	0	0
Tommy[3]	1964	A	23	6	5	0	1
	1965	A	12	11	19	0	0
Matilda	1964	A	6	1	17	0	0
Rasmunda[4]	1964	A	21	14	0	17*	1
Anna-K[3]	1964	Y	32	4	25	0	1
	1965	A	26	19	16	0	0
Lola[5]	1964	Y	11	0	4	16	0
	1965	A	19	0	1	0	0
Millie	1964	Y	3	0	3	2	0
P-G	1965	Y	17	2	0	0	0
Catlin	1964	F	0	0	1	0	0
	1965	Y	7	0	0	0	0
Cry-baby[4]	1964	F	5	1	16	9*	0
Hades	1964	F	1	2	0	0	0
	1965	Y	7	0	15	10	0
Bill	1964	A	3	0	0	0	4
Oscar[5]	1964	Y	26	0	20**	0	0

---

1 All females except Bill and Oscar.
2 Abbreviations: A-adult; Y-yearling; F-fawn.
3 Regularly associated in 1965.
4 Mother and daughter.
5 Probably siblings.
* All observations of the same unmarked deer - a spikehorn believed to be a yearling.
** Mostly observations with Lola.

Table 29. Descriptive statistics for length of swimming periods of adult males and other deer in Deer Lake, June-August, 1965.

Statistic	Adult Males	Females And Immature Males
Number of Observations	42	75
Range	2.4 - 71.0*	2.6 - 44.9
Mean	24.8	13.1
95% Confidence Interval	19.7 - 29.9	11.1 - 15.1
Standard Deviation	16.5	8.5
Variance	271	72

*Times are in minutes and tenths.

APPENDIX I

Table 30. Common and scientific names of plants included in the text.

Common Name	Scientific Name[1]
Beech	*Fagus grandifolia*
Sugar Maple	*Acer saccharum*
Striped Maple	*Acer pennsylvanicum*
Paper Birch	*Betula papyrifera*
Yellow Birch	*Betula alleghaniensis*
Balsam Fir (Fir)	*Abies balsamea*
Hemlock	*Tsuga canadensis*
Spruce	*Picea* spp.
Red Spruce	*Picea rubens*
White Cedar (Cedar)	*Thuja occidentalis*
White Pine	*Pinus strobus*
Alder	*Alnus incana*
Willow	*Salix* spp.
Witch-hobble	*Viburnum alnifolium*
Raspberry	*Rubus* sp.
Water Shield	*Brasenia schreberi*
Bladderwort	*Utricularia* spp.
Bracken Fern	*Pteridium aquilinum*

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[1] Scientific names of trees according to Little, 1953. Scientific names of other plants according to Fernald, 1950.

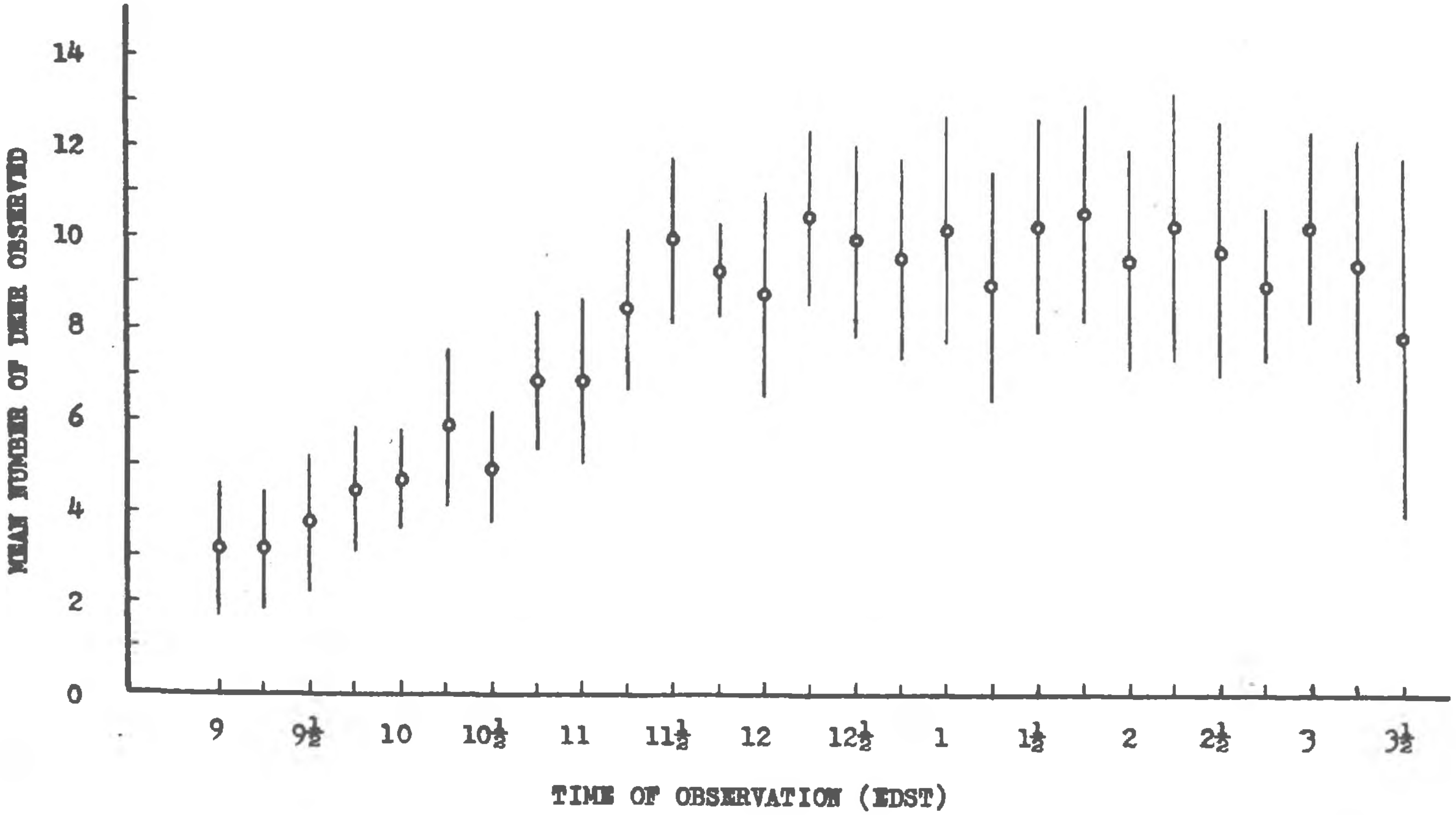

Figure 11. Mean numbers of deer observed at Deer Lake at 15-minute intervals from 9:00 AM through 3:15 PM, June-August, 1965. (The lines around the plotted means delineate the 95% confidence intervals)

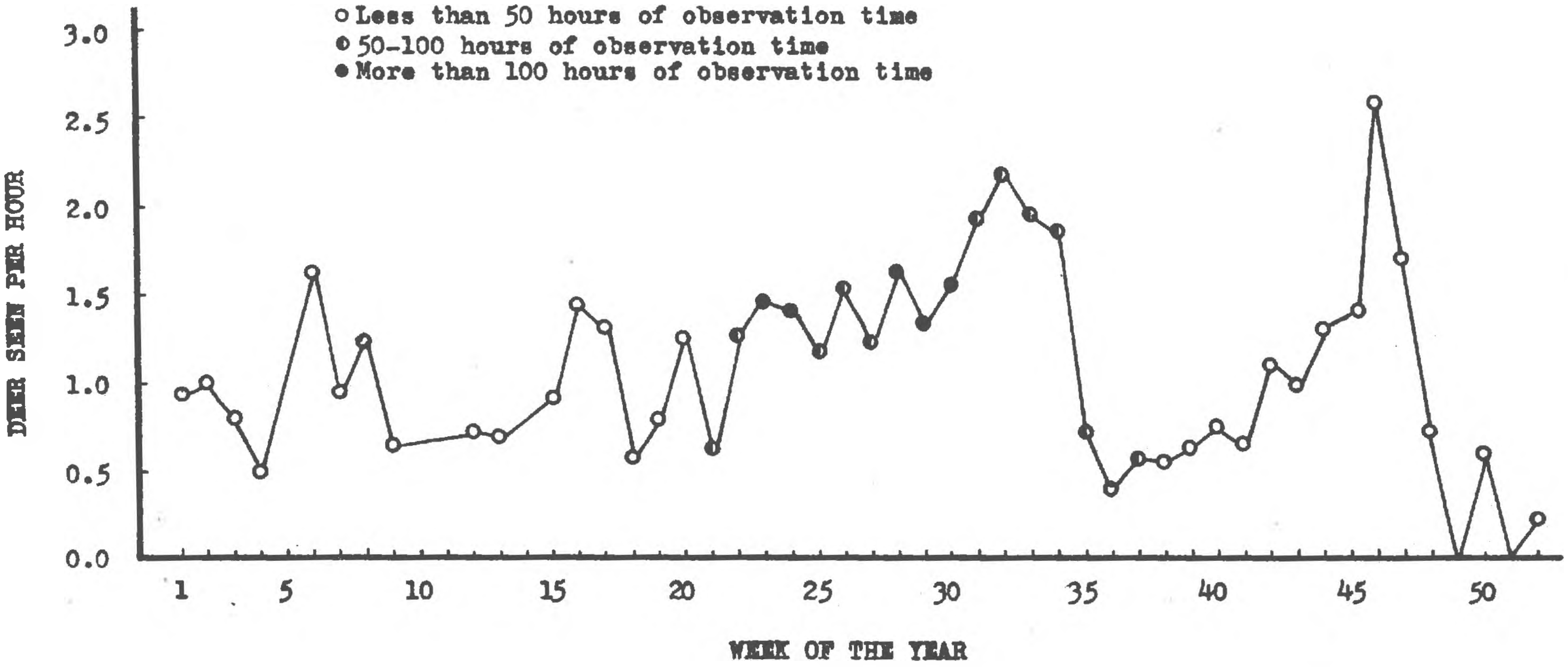

Figure 12. Number of deer observed per hour each week from June, 1963-September, 1965, based on 2656 roadside observations.

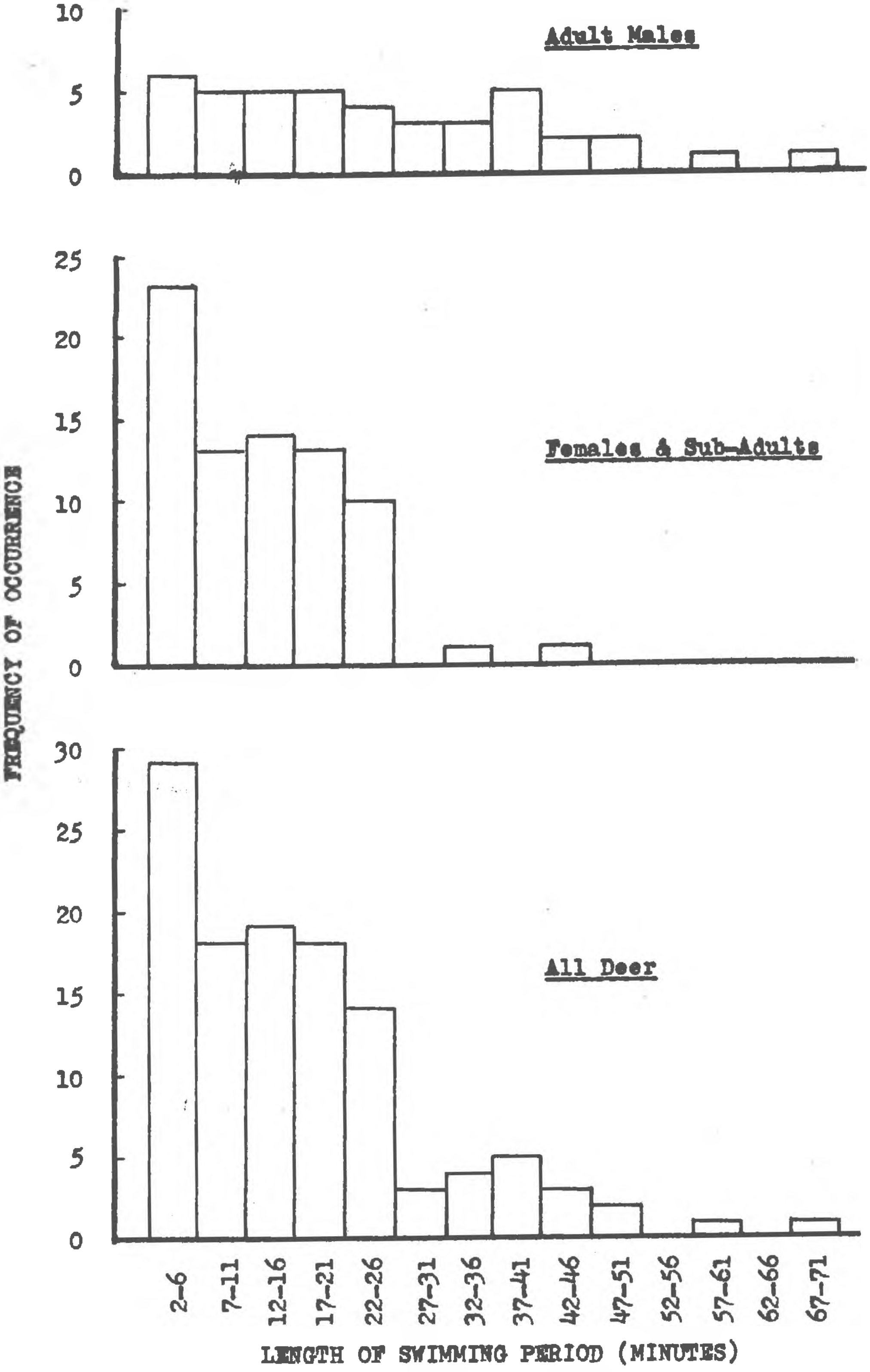

Figure 14. Frequency distributions of lengths of swimming periods for deer in Deer Lake, June–August, 1965.

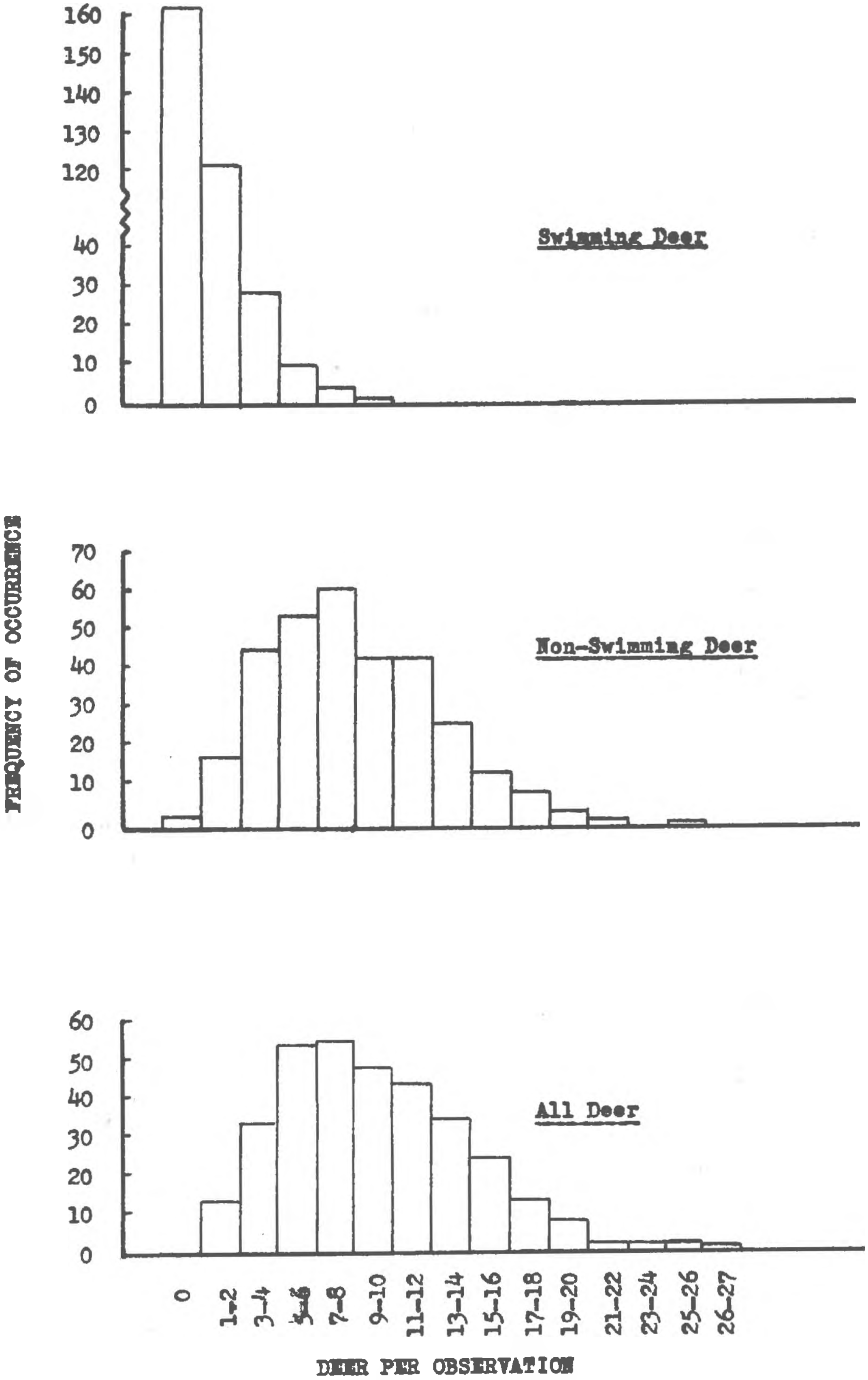

Figure 13. Frequency distributions of numbers of deer observed at Deer Lake at 15-minute intervals from 11:15 AM through 3:15 PM, June-August, 1965.

Table 24. Simple, partial, and multiple correlation coefficients for number of deer seen at Deer Lake with day of observation, temperature, relative humidity, and wind, summers of 1964 and 1965.[1]

Variable	Simple Correlation Coefficient	Partial Correlation Coefficient	Multiple Correlation Coefficient (R)	R^2
1964				
Day of Observation	-0.54^{**}	-0.18	-	-
Relative Humidity %	-0.65^{**}	-0.48^{**}	-	-
Temperature °F.	0.50^{**}	0.15	-	-
Wind mph	0.19	0.16	-	-
All Combined	-	-	0.72^{*}	0.52
1965				
Day of Observation	-0.29^{**}	-0.24^{*}	-	-
Relative Humidity %	-0.36^{**}	-0.28^{*}	-	-
Temperature °F.	0.12	0.09	-	-
Wind mph	0.24^{*}	0.14	-	-
All Combined	-	-	0.47	0.22

[1] Based on numbers of deer seen per observation: 42 observations in 1964, 82 observations in 1965.

* t-test or F test for 0 population correlation significant at P = .05; ** at P = .01; hence these coefficients may be considered as significantly different from 0.

Table 23. Simple correlation coefficient for various measures of nighttime deer activity with day of observation.

Measure[1] Of Activity	Year(s)	Period Of Observation	Number Of Observations	Correlation Coefficient[2]
Percent of 24-hour track score in the 6 PM - 6 AM period	1963-1964	May 25-Oct 5	17	-0.78**
Track Score 6 PM - 6 AM	1964	May 25-Aug 26	12	-0.61*
Deer Seen On Spot lighting Counts	1964	May 26-Aug 27	17	-0.69**
Deer Seen On Spot lighting Counts	1965	May 25-Aug 27	40	-0.63**

1 Track score is number of 5-chain sections with tracks.

2 The chi-square test for homogeniety of correlation coefficients was not significant at P = .05, hence the coefficients may be considered homogeneous.

* t-test for 0 population correlation significant at P = .05; ** at P = .01; hence these coefficients may be considered as significantly different from 0.

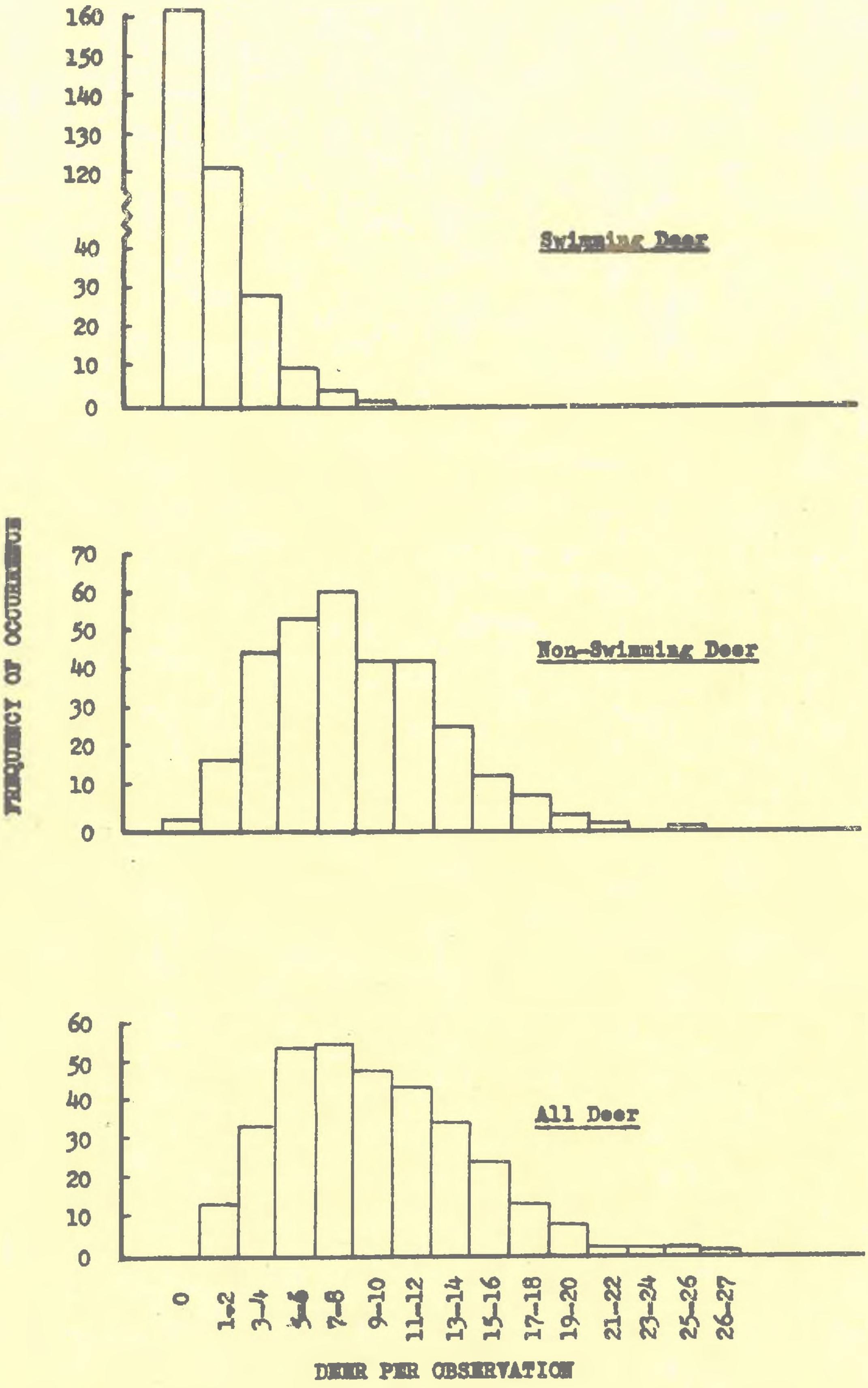

Figure 13. Frequency distributions of numbers of deer observed at Deer Lake at 15-minute intervals from 11:15 AM through 3:15 PM, June-August, 1965.

Table 28. Density of water shield on the surface of Deer Lake in June and August, 1964.

Sample Bed Number	June			August		
	Sample Size	Mean Density[1]	Confidence Interval (95%)	Sample Size	Mean Density	Confidence Interval (95%)
1	10	8.7	6.4 - 11.0	10	47.4	30.4 - 64.4
2	10	11.5	6.3 - 16.7	9	40.9	34.0 - 47.8
3	10	17.2	11.5 - 22.9	10	109.0	97.3 -120.7
4	10	8.1	3.1 - 13.1	10	61.7	40.9 - 82.5
5	10	14.5	9.1 - 19.9	10	71.3	47.7 - 94.8
6	10	9.4	5.9 - 12.9	10	66.3	39.7 - 92.9
Total	60	11.6	9.8 - 13.3	59	66.5	57.7 - 75.3

[1] Density based on number of floating leaves per 6.1 square foot sampling hoop. Density per square foot equals tables figures divided by 6.1.

Table 24. Simple, partial, and multiple correlation coefficients for number of deer seen at Deer Lake with day of observation, temperature, relative humidity, and wind, summers of 1964 and 1965.[1]

Variable	Simple Correlation Coefficient	Partial Correlation Coefficient	Multiple Correlation Coefficient (R)	R^2
1964				
Day of Observation	-0.54**	-0.18	-	-
Relative Humidity %	-0.65**	-0.48**	-	-
Temperature °F.	0.50**	0.15	-	-
Wind mph	0.19	0.16	-	-
All Combined	-	-	0.72*	0.52
1965				
Day of Observation	-0.29**	-0.24*	-	-
Relative Humidity %	-0.36**	-0.28*	-	-
Temperature °F.	0.12	0.09	-	-
Wind mph	0.24*	0.14	-	-
All Combined	-	-	0.47	0.22

---

[1] Based on numbers of deer seen per observation: 42 observations in 1964, 82 observations in 1965.

* t-test or F test for 0 population correlation significant at P = .05; ** at P = .01; hence these coefficients may be considered as significantly different from 0.

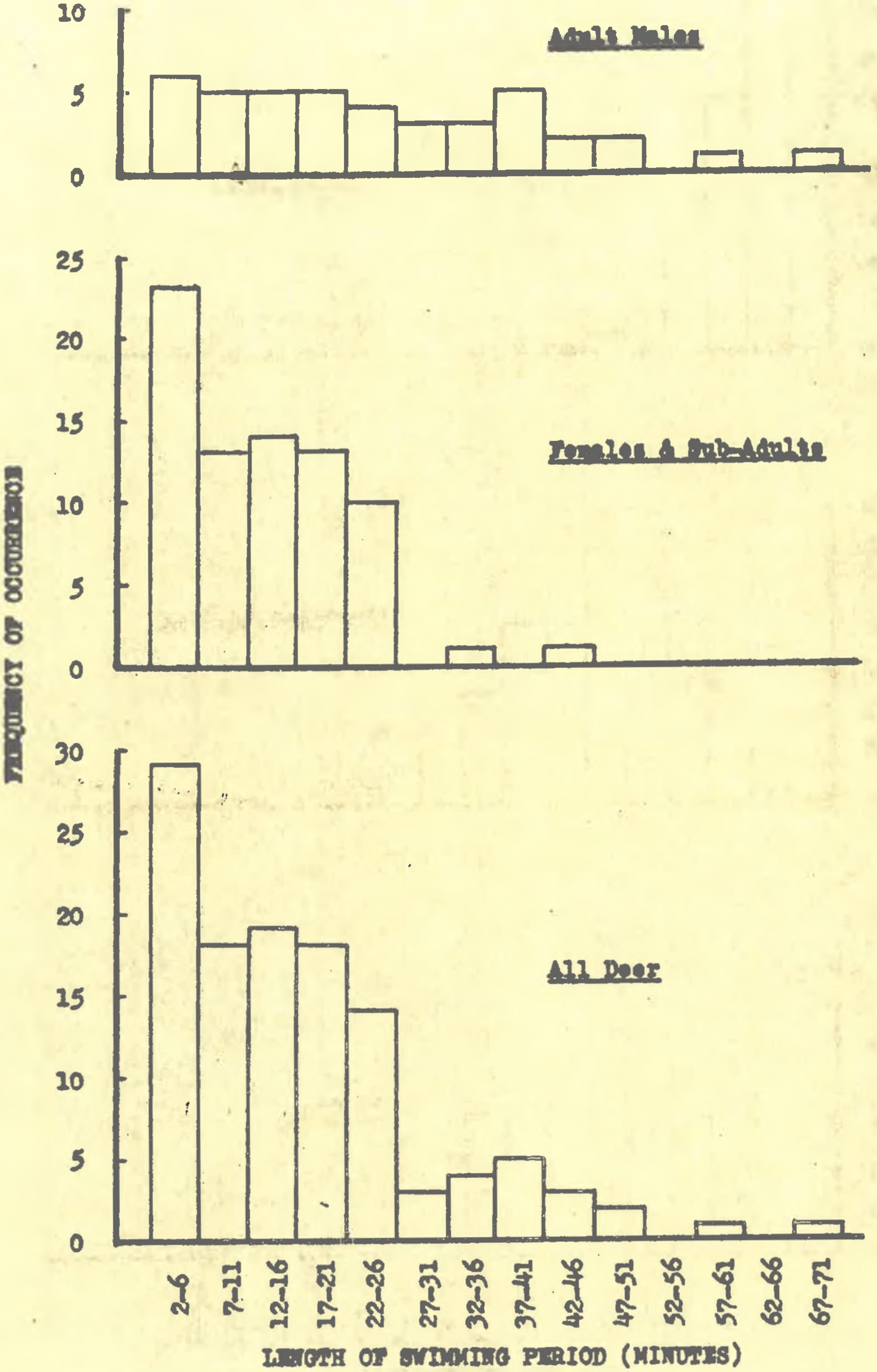

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Table 29. Descriptive statistics for length of swimming periods of adult males and other deer in Deer Lake, June-August, 1965.

Statistic	Adult Males	Females And Immature Males
Number of Observations	42	75
Range	2.4 - 71.0*	2.6 - 44.9
Mean	24.8	13.1
95% Confidence Interval	19.7 5.1 19.7 - 29.9 24.8 5.1	11.1 - 15.1
Standard Deviation	16.5	8.5
Variance	271	72

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*Times are in minutes and tenths.

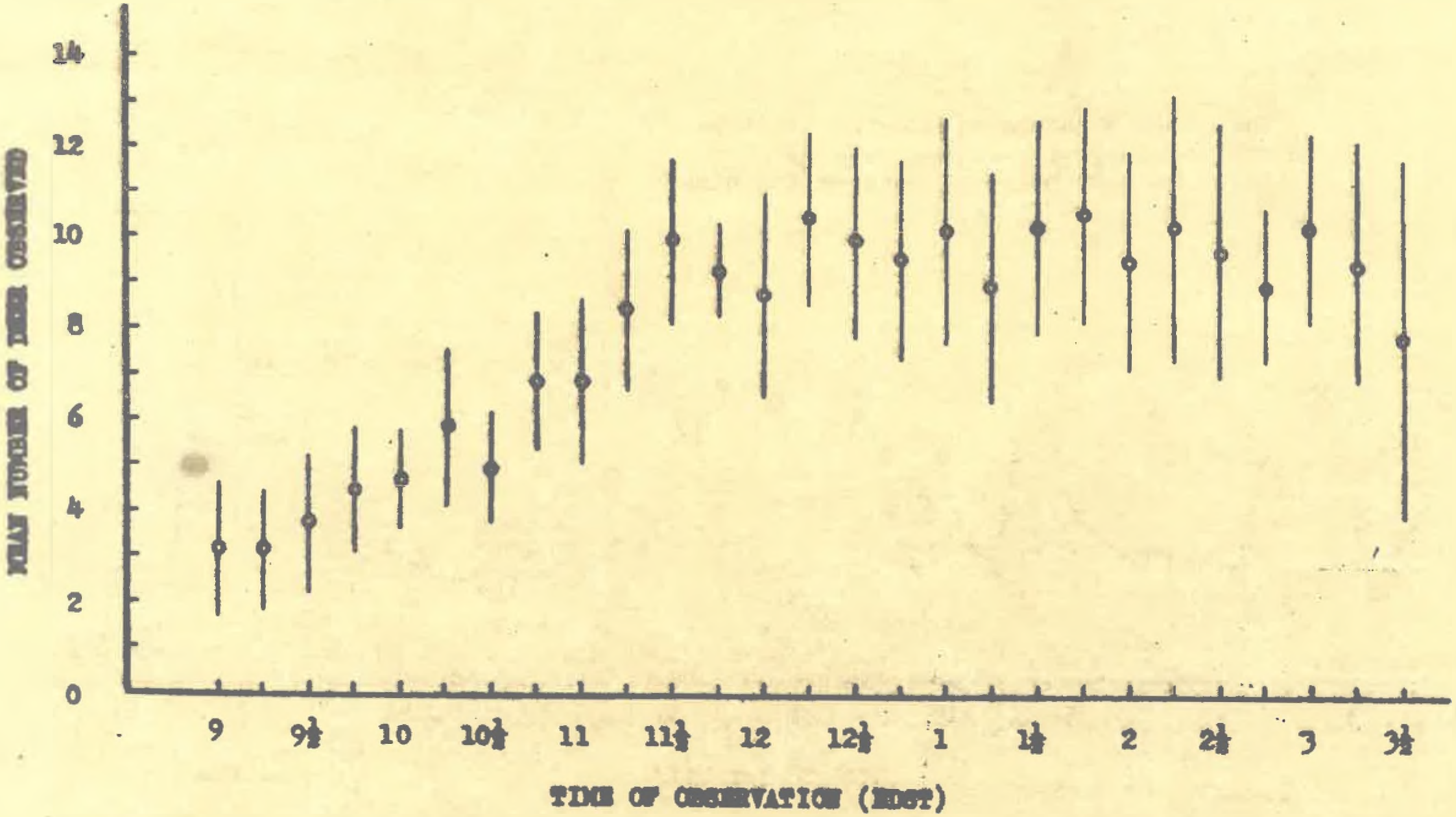

Figure 11. Mean numbers of deer observed at Deer Lake at 15-minute intervals from 9:00 AM through 3:15 PM, June-August, 1965. (The lines around the plotted means delineate the 95% confidence intervals)