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SEASONAL MIGRATIONS AND MORTALITY OF WHITE-TAILED DEER IN MICHIGAN'S UPPER PENINSULA

By

Timothy Richard Van Deelen

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

1995

UMI Number: 9605961

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ABSTRACT

SEASONAL MIGRATIONS AND MORTALITY OF WHITE-TAILED DEER IN MICHIGAN'S UPPER PENINSULA

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The management of white-tailed deer (Odocoileus virginianus) populations in Michigan's Upper Peninsula needs to be balanced with other land uses in the region. The integration of deer management goals into the broader forest management is complicated because; 1) northern deer may migrate between distant summer ranges and winter concentration areas (deeryards), and 2) variations in winter severity can severely affect deer mortality apart from management action.

In this study I describe the migration and mortality patterns of deer that winter in 2 regionally-important deeryards on the Hiawatha National Forest. Over a 4-year period, 507 deer were captured and ear-tagged. Ninety-five (all age and sex classes) were radio-collared and located to determine migration patterns and cause-specific mortality. Distance, direction, and timing of spring migrations were compared among sex and age classes and between years and deeryards. Results suggested that the deer using a given deeryard have characteristic movement patterns that remain similar from year to year. Overlap on the summer range of deer from different herds suggested that for northern deer, population structure may be partially a function of the spatial arrangement of summer and winter ranges in the landscape.

Cause specific mortality patterns were compared among sex and age classes.

Results indicated that the sex and age structure of Upper Peninsula deer was a result of bucks-only hunting regulations. Annual survival for yearling and adult bucks was significantly lower ($P < 0.05$) than that of yearling and adult does, with hunting as the chief source of mortality. Simulation models suggested that mortality regimes characteristic of male-biased hunting may cause population-wide increases in inbreeding and a loss of heterozygosity over a range of deme sizes.

The components of the thermal-cover sub-model of a Habitat Suitability Index model showed poor or weak correlations with pellet-group counts in the study area deeryards. Study design, variation in the pellet-group index, and scale issues may have precluded an adequate test of the sub-model. Modifications to make the model a better descriptor of the study area deeryards are discussed.

Resolution of the problems inherent with managing northern deer and their habitat requires a landscape-scale approach that integrates information about migration tradition, demographics, and seasonal habitat use.

ACKNOWLEDGMENTS

I thank Drs. Jon Haufler (Chair), Rique Campa, Kurt Pregitzer, Don Straney, and Scott Winterstein for serving on my graduate committee and for ushering me through this final part of the grad school process. Special thanks goes to Jon who worked hard to be available despite the mileage between Boise and MSU, and to Rique who cheerfully filled the role of Major Professor in Jon's absence. I'm also grateful to the other faculty who took interest in me and my research - notably Drs. Harold Prince and Darrell King.

This research was funded by UP Whitetails Assn. Inc. (UPW, an Upper Peninsula deer hunter's group) and the Hiawatha National Forest - to whom I am very grateful. I Also appreciate the support of the Michigan Department of Natural Resources through access to their data and experts.

This project couldn't have been done without UPW's deer trapping program. UPW members Al Ettenhoffer, Pete Jandro, Don Seymour, Joe Vardian, Russ Brown, Tim Kobasic, and the Verbrigge family deserve special recognition for the many hours of volunteer labor given. The entire UPW membership deserves high praise for its willingness to give so freely of their time and money for conservation research.

I grateful to the staff of the Hiawatha's Rapid River Ranger Station for making my yearly stays in the U.P. so enjoyable. Special recognition goes to Maya Hamady for shepherding the deer project through any administrative hurdles that cropped up. In addition to being a good friend, Maya is a better biologist and researcher than most people realize. Special recognition also goes to Paul Thompson for the many hours of field work and for the reliably good company. Paul took personal ownership of the deer project when I was in Lansing and looked after it as if it were his own. Thanks also to Doris Gerdes for her friendship and interest.

Many others helped with field work and I thank them all; Mark Parkinson, Kimberly Smith, Tony Duffiny, Teresa Mackey, Jason Halifax, Sherry DeLong, Joe Vardian, Jerry Terrian, Mark St. Auben, Gerald Nyberg, Mary Clement, and Loma Steinhoff.

I'm grateful to my fellow grad students for their friendship and good humor, especially that of John Niewoonder, Steve Negri, Gary Roloff, Bill Bowerman, and Brian Kernohan.

My time was split between course work at MSU and field work in the U.P., so from my wife's point of view I was either surly or absent. My dear wife Carol put up with it all with grace and patience. I thank her for her love and support.

I thank my parents (Dick and Jan Van Deelen) and Carol's parents (Bob and Hope Dejonge) for their inspiration and support of us through 7 years of grad school.

Finally, I thank God.

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INTRODUCTION

Nearly extirpated in many areas during the late 1800s because of unregulated hunting and habitat destruction, white-tailed deer (Odocoileus virginianus) populations have rebounded thanks to increasing second growth and edge habitats, and wildlife management programs (McCabe and McCabe 1984). Indeed, the white-tailed deer's secretive nature and fondness for second growth, edge, and farmlands make it well adapted to human-influenced environments if given adequate protection from over-harvest.

In 1993 in Michigan, around 310,000 bow-hunters, 750,000 rifle hunters, and 150,000 muzzle-loader hunters spent around 10 million days in the field hunting deer (Michigan Department of Natural Resources 1993). Langenau (1979) reported that people from all walks of life value encounters with wild deer whether actively sought or incidental to other outdoor activity. Deer hunters spent approximately 350 million dollars in 1991 (Michigan Dept. of Natural Resources 1991), underscoring the white-tailed deer's importance to Michigan.

Deer populations in the Upper Great Lakes Region have risen generally in spite of concerns about the negative effects of deer herbivory on commercial timber production (Horton 1964, Anderson and Loucks 1979, Miller 1990, Pregitzer 1990) and their own range (Aldous 1941, Dahlberg and Guettinger 1956, Verme 1965).

Prolonged browsing at high deer densities can reduce seedling recruitment and impact the regeneration of commercial tree species such as northern white cedar (Thuja occidentalis, Verme and Johnson 1986, Miller 1990, Pregitzer 1990) and eastern hemlock (Tsuga canadensis Anderson and Loucks 1979, Alverson et al. 1988). Browsing can also reduce seedling recruitment from layering and tree tipping that may facilitate cedar persistence in a stand (Pregitzer, 1990). Similar problems occurred in hardwoods stands in Pennsylvania (Tilghman 1989). In Michigan's Upper Peninsula, the Hiawatha National Forest has issued a partial moratorium on cedar harvest until regeneration problems can be solved.

More recently, ecologists have become concerned about the effects that deer herbivory may be having on the structure and composition of the plant communities that make up the northern forest (Alverson et al. 1988) . Herbaceous species and shrubs may be especially vulnerable to deer herbivory because they never grow beyond the reach of deer. Canada yew (Taxus canadensis), an understory shrub once common in the northern forests is now locally extinct in areas of high deer use (Alverson et al. 1988). Habeck (1960) included Canada yew in a list of 10 conifer swamp plants in Wisconsin that are "moderate decreasers" in the presence of deer herbivory. He listed an additional 10 "extreme decreasers" that are even more sensitive to browsing. Ninety-eight threatened and endangered plants from 36 families across the United States are threatened by deer herbivory (Miller et al. 1992). Alverson et al. (1988) described deer herbivory as an edge effect of forest fragmentation that might contribute to a region-wide homogenization of the northern forests.

Dense conifer "deeryards" are the principle habitat requirement for the winter survival of deer in the northern part of their range (Bartlett 1938, Verme 1965). Deeryards are areas were dense conifer overstories are used as winter range for concentrations of wintering deer. In the Upper Great Lakes Region, most yards are in areas where mature cedar or swamp conifer stands predominate (Blouch 1984). Deeryard overstories facilitate winter survival by providing deer a thermal barrier to the night sky and by providing shelter from winter winds, reducing the loss of energy by radiation and convection (Verme 1965, 1968, Ozoga 1968, Ozoga and Gysel 1972, Moen 1976, Blouch 1984). Another energetic advantage is the amount of snow intercepted by the overstories. Lower deeryard snow depths relative to non-deeryard areas reduce energetic costs incurred by moving and foraging (Verme 1965, Ozoga 1968, Ozoga and Gysel 1972, Moen 1976). The concentrations of deer themselves are similarly adaptive because trail systems develop which further reduce the energetic costs of foraging and movement (Verme 1965, 1968). Winter concentrations and deeryard trail systems may also be adaptive as an anti-predator strategy because the trail systems facilitate escape from canid predators and concentrations lower the predator : prey ratio (Messier and Barrette 1985). Hoskinson and Mech (1976) and Nelson and Mech (1981) found higher survival among deer whose deeryards were located at the margins of adjacent wolf-pack territories. Nelson and Mech (1981) argued that wolf predation and not energy conservation was the selective force that shaped yarding behavior in northern white-tailed deer.

The cedar itself provides highly nutritious, palatable browse and cedar browse has often been suggested as an important component of the survival advantage conveyed by conifer swamp deeryards (Aldous 1941, Verme 1965, Ullrey et al. 1967). In fact, very little cedar browse (indeed very little browse of any kind) is available in the understories of many traditionally-used deeryards. Most deeryards are browsed to the height that a deer can reach, and available cedar browse is limited to occasional blow-downs (Blouch 1984). Much cedar browse is made available from the tops and slash left at winter cuttings, and winter cutting has been suggested as a management technique to provide wintering deer with food (Aldous 1941, Verme 1965). This is a questionable management technique because swamp conifer stands are nearly impossible to regenerate in the presence of intense deer use, and because winter browse availability may be less important than shelter and environmental factors in determining deer survival (Ozoga and Verme 1970).

Northern deer depend on fat reserves for winter survival (Mautz 1978). Even when food is provided ad libitum, deer decrease their intake and begin to lose weight during the winter (Silver et al. 1969, Ozoga and Verme 1970, Moen 1978). Wintering deer avoid areas of poor shelter even though browse may be plentiful (Verme 1965). Survival depends on minimizing exposure to maintain energy reserves until green-up (Ozoga 1968, Ozoga and Verme 1970). Late springs and severe winters are the biggest killers (Ozoga and Verme 1970, Moen 1978, Blouch 1984) and winter browse, which is relatively poor in quality, serves mainly to decrease the rate of winter weight loss (Mautz 1978).

Management of the cedar and swamp conifer types has involved small clear-cuts

(Aldous 1941) or alternating strip cuts (Verme 1965) in a matrix of mature timber, a regeneration technique designed to provide harvested areas with an abundant seed source. Verme (1965) recommended removal of the remaining mature timber as soon as regeneration was established in the earlier cuttings to provide open areas large enough to exclude wintering deer and to prevent deer from browsing the regenerating cedar. Verme and Johnson (1986) reported that block clear-cuts may be easier to manage than strip clear-cuts, and that broadcast burning of the logging slash may enhance cedar regeneration under certain conditions. Most instances of "failed regeneration" in yarding areas are probably due to the failure to remove remnant strips once regeneration has started in the clear-cut areas (Verme and Johnson 1986).

Deer populations in the central upper peninsula have, in a sense, been managed since 1837 when logging began near Escanaba (Langhorne 1988). Van Deelen et al. (1995) described how deer populations in the upper peninsula have responded to expanded summer range, a by product of logging patterns since the 1840s. Except for a brief period around 1900, deer populations have been consistently and significantly higher than they were prior to European settlement (MDNR no date, Langenau 1994).

In 1859, the state of Michigan enacted the first deer hunting season. The first deer hunting license and bag limit (in 1895) and the first bucks-only restrictions (in 1921) followed (Bennett et al. 1966). Langenau (1994) noted that bag limits ended market hunting and brought harvest management under the purview of the state. He stated that 1895 was the beginning of formal management of deer populations. The timing of hunting seasons, bag limits, and restrictions on taking certain age or sex classes remain the deer manager's primary tools in regulating harvest management. By 1941, the Michigan Department of Conservation was experimenting with liberalized doe-harvests in response areas that were perceived to be over-populated with deer (Bennett et al. 1966). Public reaction to doe hunting during the early 1950's was extremely negative as doe harvests coincided with deer populations that were declining due to successional changes on the summer range (Langenau 1994).

Today, the Michigan Department of Natural Resources (formerly the Department of Conservation) maintains strict control of the harvest of does by issuing a limited number of "doe permits" in select deer management units to be used during the firearm hunting season. By contrast buck harvesting is not restricted by management unit, number of permits (licenses) issued or hunting season (archery, firearm, or muzzle-loader).

Reluctance to allow doe harvests is counter-productive to population reduction efforts. Population numbers are much more robust to sex-biased harvests than they are to un-biased or age-biased harvests. This is especially true of deer because of the fecundity of does and the promiscuous polygynous mating system (Caughley 1977, McCullough 1984).

McCullough (1984) recommended that sustainable harvest regimes be designed based on a knowledge of the recruitment rate of the population and the carrying capacity of the population's habitat which he assumed to be constant. Unfortunately for the managers of northern Michigan deer, the carrying capacity of the Upper Peninsula varies in response to successional changes, timber markets and weather. Recruitment in Upper

Peninsula deer herds is largely a function of winter severity and fluctuates as well. By default, deer management is somewhat reactionary, being driven by perceptions of habitat damage and public opinion. Concern that deeryards are being over-browsed and suggestions that deer harvests be used to alleviate over-browsing are recurring themes (ie. Bartlett 1938, Aldous 1941, Jenkins and Bartlett 1959, Verme 1965, Alverson et al. 1988, Miller 1990, Pregitzer 1990, Miller et al. 1992).

Management of deer - deeryard interactions are complicated by the migratory behavior of northern deer. Verme (1973) found that Upper Peninsula deer will migrate between deeryards and summer ranges that may be as much as 50 km distant. Migration routes are traditional and individual deeryards supply deer to specific areas in the matrix of surrounding uplands (Verme 1973). Migration traditions are passed from mother to daughter in the deer's matriarchal social structure (Hoskinson and Mech 1976). Verme (1973) speculated that reduction of the deer population in given yards could leave "holes" in the summer distribution of deer elsewhere.

This research was prompted by concerns over deer browsing impacts on the west unit of the Hiawatha National Forest. Swamp conifer stands on the Hiawatha National Forest act as winter deeryards for deer from throughout the central Upper Peninsula, but regeneration of cedar and other valuable timber species has been impaired due to intense and prolonged deer browsing. In addition, ecologists are concerned about the effects of deer herbivory on the swamp conifer plant communities. Deer enthusiasts worry that reduced deeryard deer densities will impact deer distributions on the summer range.

STUDY AREAS

The Whitefish deeryard and the Stonington deeryard complex (hereafter "the Stonington deeryard") were chosen as study areas. These deeryards are representative of the major deeryards found along the northern shore of Lake Michigan (Figure 1, 2). Deeryard boundaries were taken from "core deeryard" maps published by the Michigan Department of Natural Resources in 1977 (approx. Lat 45° 55'N, approx Long 86° 55'W). Similar maps from 1967 and 1958 indicated the same areas being used as deeryards. All three sets of maps described food conditions in the yards as "poor", an indication of little available browse. The yarding areas are located in central Delta County, in Michigan's Upper Peninsula.

The Stonington yarding area lies on the Stonington peninsula. It is in the Escanaba subdistrict (region III) of a regional ecosystem classification of Michigan (Albert et al. 1986) and has a cool, lacustrine climate with a cool but relatively long growing season (125 days). Annual precipitation is 810 mm. Mean temperature from May to September is 14.9 C, and annual extreme minimum temperature is -29 C (Albert et al. 1986). Surficial geology consists of low elevation (177m) glacial lake plains, outwash plains, and till plains. Nearly level, poorly to very poorly drained organic soils with some sand, and sandy loams lie over limestone bedrock (Berndt 1977, Albert et al. 1986).

The Whitefish yarding area lies on the floodplain of the lower drainage of the Whitefish river watershed. It falls on the boundary of the Hermansville, Seney, and Escanaba ecosystem subdistricts (regions III, IV; Albert et al. 1986) and has less

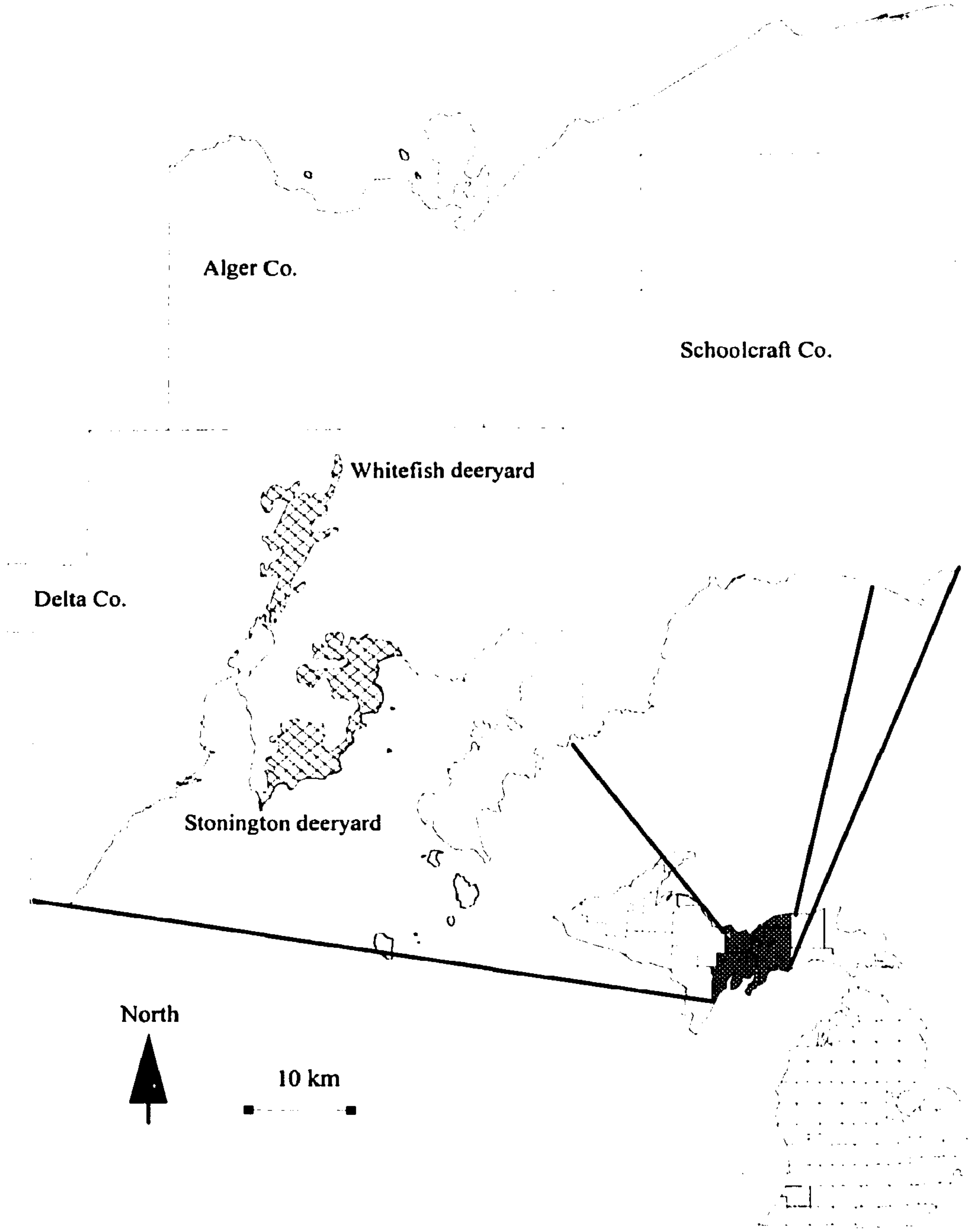


Figure 1. Study area map showing the Whitefish and Stonington deeryards. Inset shows the location of the 3-county study area in Michigan's upper peninsula.

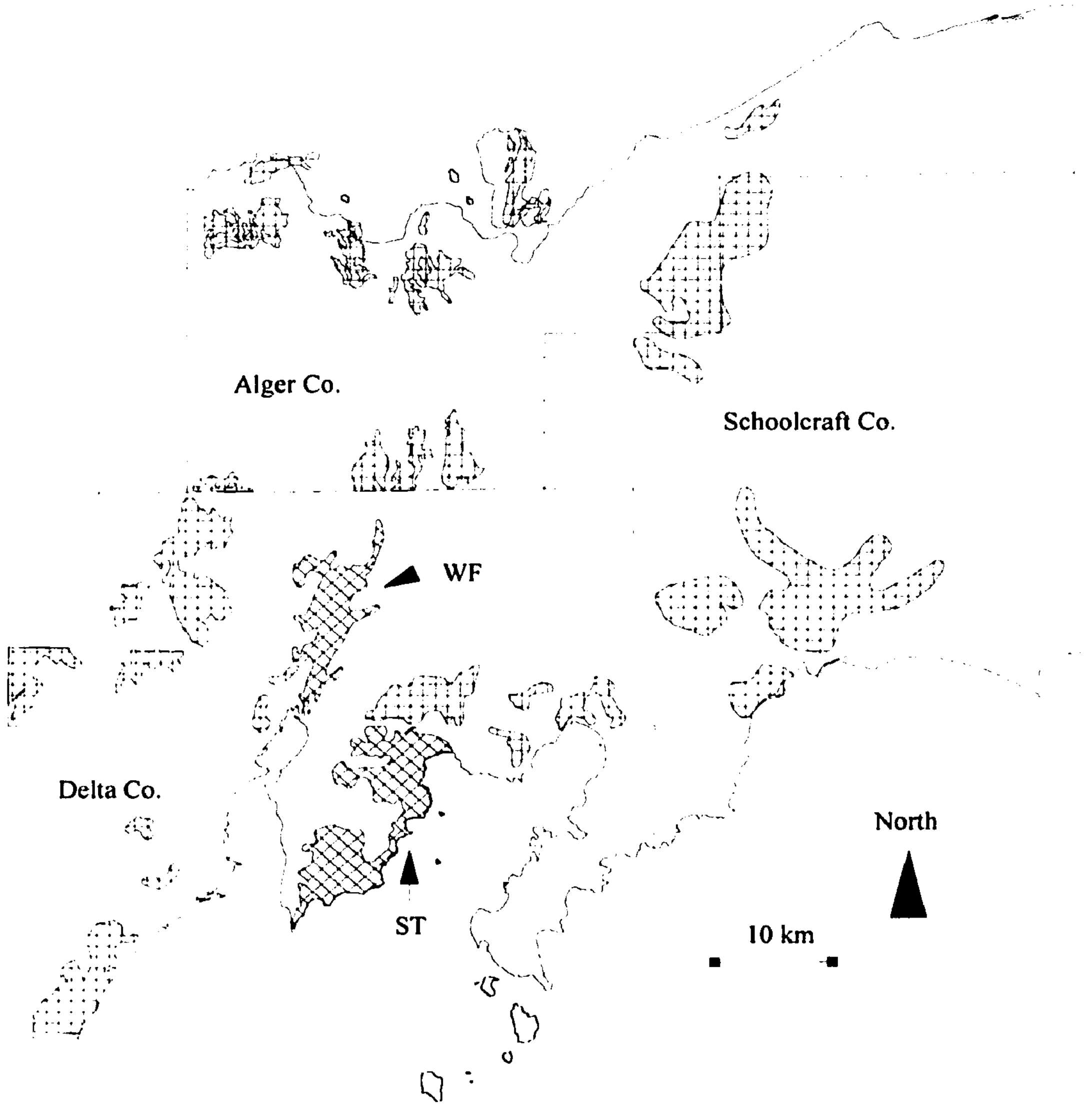


Figure 2. The Whitefish (WF) and Stonington (ST) deeryards in relation to other known deeryards in the study area.

lacustrine influence than the Stonington yarding area. The growing season is 107 - 125 days. Annual precipitation is 800 - 840 mm. Mean temperature from May to September is 14.4 - 15.7 C, and annual extreme minimum temperature is -28 to -29 C (Albert et al. 1986). Surficial geology is sand lake plain, and outwash plain, bounded by ground moraines and drumlins to the west. Nearly level, very poorly to relatively well drained organic soils lie over sand, gravel, or limestone bedrock (Berndt 1977, Albert et al. 1986).

Extensive stands of cedar-dominated conifer swamps make these areas valuable as deeryards. Current land use is mostly forest-oriented. Ownership is scattered private holdings and National Forest. A few small active and abandoned farms are located on the Stonington peninsula. Existing forests are second-growth after the intense fires that followed the large-scale timber harvesting of the late 1800s (Stearns 1990). Smaller-scale logging of the second-growth forest continues to the present.

The portion of the Upper Peninsula that surrounds the study area deeryards is bounded to the north by Lake Superior and to the south by Lake Michigan. Soils are of glacial origin and consist of poorly-drained sand lake plains, outwash plains, drumlins, and end and ground moraines. The dominant upland timber type is northern hardwoods with pines on some of the drier sites. Scattered swamps, bogs, and marshes are common (Albert et al. 1986).

During the winter north winds crossing Lake Superior produce snow showers along the Lake Superior shore line. Mean annual snowfalls exceed 130 in. (333 cm) along Lake Superior. Inland snow depths average 100 in. (256 cm) and snow depths along the Lake Michigan shoreline average 55 in. (141 cm). The net effect is one of a snow depth gradient increasing from south to north. Spring conditions may be delayed as warm southerly winds are cooled by Lake Michigan (Berndt 1977).

OBJECTIVES

Specific objectives of this study were:

1. Determine the importance of the Whitefish River and Stonington Peninsula deeryards to the summer/fall distributions of deer in the central Upper Peninsula.

2. Evaluate the effects of potentially reduced winter deeryard densities on the summer deer distribution.

3. Evaluate the spatial organization of migratory deer populations in the central Upper Peninsula.

4. Compare the migratory and survival characteristics of Upper Peninsula deer populations under high density/low predation with the current model for northern deer developed in Minnesota under low density/high predation conditions.

5. Test the winter habitat sub-model in a Habitat Suitability Index model for deer in the upper Great Lakes (Bender and Haufler 1990).

The analysis is divided into 3 chapters: Chapter 1. treats movement tradition and landscape-scale management of deer and their habitat (objectives 1. and 2.), Chapter 2.

treats the population dynamics and structure of Upper Peninsula deer (objectives 3. and 4.) and Chapter 3. is a test of the winter habitat sub-model (objective 5.).

Chapter 1: Migration tradition and use of the landscape by white-tailed deer in Michigan's Upper Peninsula.

On the Hiawatha National Forest, managers are mandated with protecting the biological diversity of the native ecosystems while at the same time providing multiple use benefits such as timber, hunting opportunities, and recreation. Managers and deer hunters both recognize that the Hiawatha National Forest's Whitefish and Stonington deeryards are very important to the winter survival of deer from throughout the central Upper Peninsula. Foresters recognize regeneration problems that probably come from the intense browsing associated with wintering deer (Pregitzer 1990). Survey records from the 1850's suggest compositional changes in the overstory and understory which are consistent with deer herbivory (Van Deelen et al. unpublished data).

One obvious solution to regeneration problems and overly-intense deer herbivory would be to maintain the deer populations that use these deeryards at lower densities. However, deer in the Upper Peninsula, as well as deer in other northern climates are known to migrate between summer and winter ranges that may be up to 50km apart (Verme 1973). Moreover, patterns of seasonal range use appear to be rigidly traditional such that switching from one traditionally-used deeryard to the next is unlikely. The net effect is that reducing deer densities on a given deeryard long enough to facilitate timber regeneration beyond the point where it is vulnerable to browsing may cause persistently reduced deer densities over a large portion of the summer range.

Evaluation of proposed management solutions requires information on deer migration at two spatial scales. The fundamental social units in white-tailed deer are small matriarchal family groups (for does) and small bands of unrelated yearlings and adults (for bucks, Severinghaus and Cheatum 1956, Hawkins and Klimstra 1970, Hirth 1977). These social units migrate together (Nelson and Mech 1981). Management of the a population which winters in a given deeryard requires knowledge of migration patterns of the larger aggregation of social units (first spatial scale). Management also requires knowledge of how deer populations which use different deeryards use the landscape relative to one another, and relative to other landscape features (second spatial scale).

Managers and volunteers have been studying deer migration in the Upper Peninsula since 1932 (Bartlett 1932) by trapping deer on their winter ranges, releasing the deer with ear tags, and compiling the locations of sightings and harvests of ear-tagged deer on the summer range. Since 1989, a hunter's group known as U. P. White-tails Assn. Inc. has maintained a trap-tag-release program in cooperation with the Michigan Department of Natural Resources. Trap-tag-release programs provide valuable information on the movements of deer and have fostered a spirit of cooperation and mutual respect among deer hunters and deer managers. But because the data depend on chance sightings and hunter reports, biases are likely.

In this chapter, I describe the distance, direction, tradition, and seasonal ranges of deer that winter in the Whitefish and Stonington deeryards. Descriptive statistics are used to determine if the deeryard-specific populations move as single units. Lastly, I evaluate trap-tag-release programs by comparing them to information obtained via radio-telemetry.

Methods

In the winter of 1990-91, UP Whitetails Assn. Inc. began trapping and ear-tagging deer in or immediately adjacent to the Whitefish and Stonington deeryards (Figure 1). Trapping continued through the winter of 1993-94. Trap sites were active timber cuttings because wintering deer are attracted to the browse provided by tops and slash (Ozoga 1972). New trap sites were selected when the incidence of "recaptured" deer became greater than the incidence of un-tagged "new" captures. Trapping began in January and continued until spring breakup (usually late March). All deer were given a serially-numbered ear-tag that was color-coded according to the deeryard where each was captured. Deer were sexed and classified as fawn, yearling, or adult on the basis of tooth wear and replacement (Severinghaus 1949, Larson and Taber 1980). Canine teeth were extracted from a sub-sample of the adults and later aged by cementum annuli (Gilbert 1966, DeYoung 1989a, Matson 1991, 1993).

Traps were Stephenson-type box traps (Rongstad and McCabe 1984), baited with corn. Clover traps (Clover 1954, 1956) were occasionally used to facilitate trapping in more remote parts of the deeryards.

Posters advertising the trap-tag-release program and asking people to report sightings of ear-tagged deer were distributed to local businesses in the central Upper

Peninsula. Personnel at USDA Forest Service ranger stations and Michigan Department of Natural Resources Field Offices compiled reports of deer sightings.

In the winters of 1991-92, 1992-93, and 1993-94, I accompanied the UP Whitetails trapping crews and outfitted a sub-sample of the ear-tagged deer with radio-collars (Telonics Inc. Mesa AZ; Lotek Engineering Inc., Newmarket Ontario). Collars were allocated among all age/sex classes and were scattered among the trapping sites each winter.

I attempted to locate each radio-equipped deer once a week from 20 January 1992 to 15 January 1995. Locations were estimated by triangulation of 2 or more bearings from known locations using hand-held, two-element yagi antennae (Telonics Inc. Mesa AZ.). Deer that could not be located from the ground were located from the air using fixed-wing aircraft. A minimum of 3 aerial searches were made for missing deer before they were considered to be censored (White and Garrott 1990). Telemetry error was estimated from the Maximum Likelihood Estimator (Lenth 1981) algorithm in LOCATEII (Pacer, Truro, Nova Scotia) for sets of locations consisting of more than 2 bearings (Nams 1990). Telemetry data were then processed into location estimates using LOCATEII.

Location records for each deer were converted to PC-ARCINFO (ESRI Redlands, CA) point coverage so that the timing of long distance movements could be determined. These estimates of the timing of spring and fall migrations were used to separate locations on the summer range from those on the winter range in subsequent analysis.

The harmonic mean center (Dixon and Chapman 1980) of each deer's summer and winter ranges were determined using TELEM88 software (Department of Wildlife Ecology, University of Wisconsin). The distance and direction between seasonal ranges was calculated from the harmonic mean centers of the seasonal ranges using common trigonometric formulae. The spatial dimensions of the seasonal ranges were estimated using the 95% adaptive kernel (Worton 1989) contours provided by CALHOME software (USDA Forest Service Pacific Southwest Forest Experiment Station, Fresno CA). The 95% adaptive kernel contours were converted to PC-ARCINFO polygon coverage to describe the yearly and seasonal overlap of seasonal ranges.

Composite winter and summer ranges for each year were constructed for Whitefish and Stonington deer by calculating the 95 and 50% adaptive kernel contours for combined samples consisting of seasonal harmonic mean range centers for each individual radio-collared deer. Composite ranges for the reported sightings of ear-tagged deer were constructed by calculating the 95 and 50% adaptive kernel contours. Composite ranges were then converted to PC-ARCINFO polygon coverages to examine spatial overlap.

Distance, direction, timing, and seasonal range dimensions associated with the movements of the radio-collared deer were examined to determine whether populations using the different deeryards move in a predictable fashion. I tested each parameter for differences with respect to sex class, age class, age/sex class, year, and deeryard. The distributions of distance, timing, and range size were non-normal (Appendix), so tests were performed using non-parametric procedures (Lehman 1975). Directional data, being from a circular distribution required, a separate class of statistical procedures

(Batschelet 1981).

I investigated the incidence of migration among the radio-collared deer using 2 definitions to objectively separate migratory deer from non-migratory deer . Under the first definition migratory deer were those whose summer and winter ranges did not overlap (Larson et al. 1978, Dusek et al. 1989). Definition 2 accounted for the wide variation in summer range size. Under this definition, migratory deer were those whose harmonic mean summer range center was greater than the upper 85th percentile of summer range diameters if one assumes that summer ranges are essentially circular. I tested for the effects of sex and deeryard on the probability of being migratory using the Mantel-Haenszel test (Sokal and Rohlf 1995).

I defined migration as traditional if seasonal ranges overlapped from one year to the next for migratory deer. Sample sizes were small because radio-collared deer had to be migratory and live long enough to establish traditional movement.

Over-winter deer numbers were estimated from pellet group counts (Eberhardt and Van Etten 1956, Ryel 1971) at 50 random plots in each of the deeryards. Within years, I tested for differences in pellet-group densities between deeryards using the Mann-Whitney U test (Lehman 1975, Wilkinson et al. 1992).

Since winter weather influences migration timing (Verme 1968, Sparrowe and Springer 1970, Verme and Ozoga 1971, Drolet 1976, Hoskinson and Mech 1976, Nelson and Mech 1981, Teirson et al. 1985, Nixon et al. 1991, Nelson 1995), I examined deer movement relative to Winter Severity Indices (Verme 1968) measured at MDNR field stations in Gladstone, and Gwinn, Michigan. Spring snow melt in the study area was tracked with 8 snow depth stations which were systematically located along a north-south axis from the southern part of the Stonington deeryard to the northern part of the Whitefish deeryard. Each snow depth station consisted of a pair of snow depth gauges, one in the open, and one under a 70% or greater conifer canopy. Snow depths were checked each week from January until all the snow in the study areas had melted.

Whitefish deer were defined as deer that were trapped on or adjacent to the Whitefish deeryard. Stonington deer were defined as deer trapped on or adjacent to the Stonington deeryard.

RESULTS

Since 1991, 507 deer were trapped and ear-tagged (Table 1.). I radio-collared 95 deer (Table 2.) and located them 4599 times. Mean error arc for triangulation was 7 degrees. Median error polygons were 10.5 ha. With 1992, 1993, and 1994 data pooled, the sex/age compositions or the trapped and radioed samples differed ($X^2 = 23.5$, df = 5, $P < 0.001$) because yearlings of both sexes were relatively under-represented in the trapped sample.

Winter Severity Indices (Figure 3) suggested that the winter conditions were more arduous during the winter of 1993-1994, than during the previous 2 winters. All three winters were mild relative to the 27 year average for the central Upper Peninsula. Spring snow depth profiles (Figure 4) indicated that March snow depths were highest in 1992, intermediate in 1993, and lowest in 1994. Midwinter snow depths increased along a south to north gradient and southern portions of the study area were snow free earlier (Table 3).

Table 1. Age and sex classification of deer trapped in the Stonington (ST) and Whitefish (WF) deeryards 1991 - 1994.

		Classification					
Year	Deeryard	Adult F.	Yearling F.	Fawn F.	Adult M.	Yearling M.	Fawn M.
1991[*]	ST	30		17	5		16
	WF	22		11	5		17
1992	ST	41	2	12	0	1	13
	WF	21	3	24	2	3	42
1993	ST	23	0	15	3	3	20
	WF	18	4	11	1	3	7
1994	ST	28	2	13	3	6	17
	WF	13	1	11	2	1	15
	Total	196	12	114	21	17	147

[*] Yearlings were counted as adults in 1991.

Table 2. Age and sex classifications of radio-collared deer. Table entries are the total number alive at the beginning of each year.

		Classification											
Year	Deeryard	Adult F.		Yearling F.		Fawn F.		Adult M.		Yearling M.		Fawn M.	
1992	ST	10	(10)[a]	0		5	(5)	0		1	(1)	5	(5)
	WF	7	(7)	1	(1)	5	(5)	2	(2)	2	(2)	5	(5)
1993	ST	12	(5)	3		5	(5)	0		1		5	(5)
	WF	8	(8)	2	(1)	6	(6)	1		4	(4)	5	(5)
1994	ST	9		5		5	(5)	0		1		5	(5)
	WF	10		4		4	(4)	3		1		5	(5)
	Total	56	(24)	15	(2)	30	(30)	6	(2)	10	(7)	30	(30)

[a] Entries in parenthesis indicated the number of new individuals radio-collared

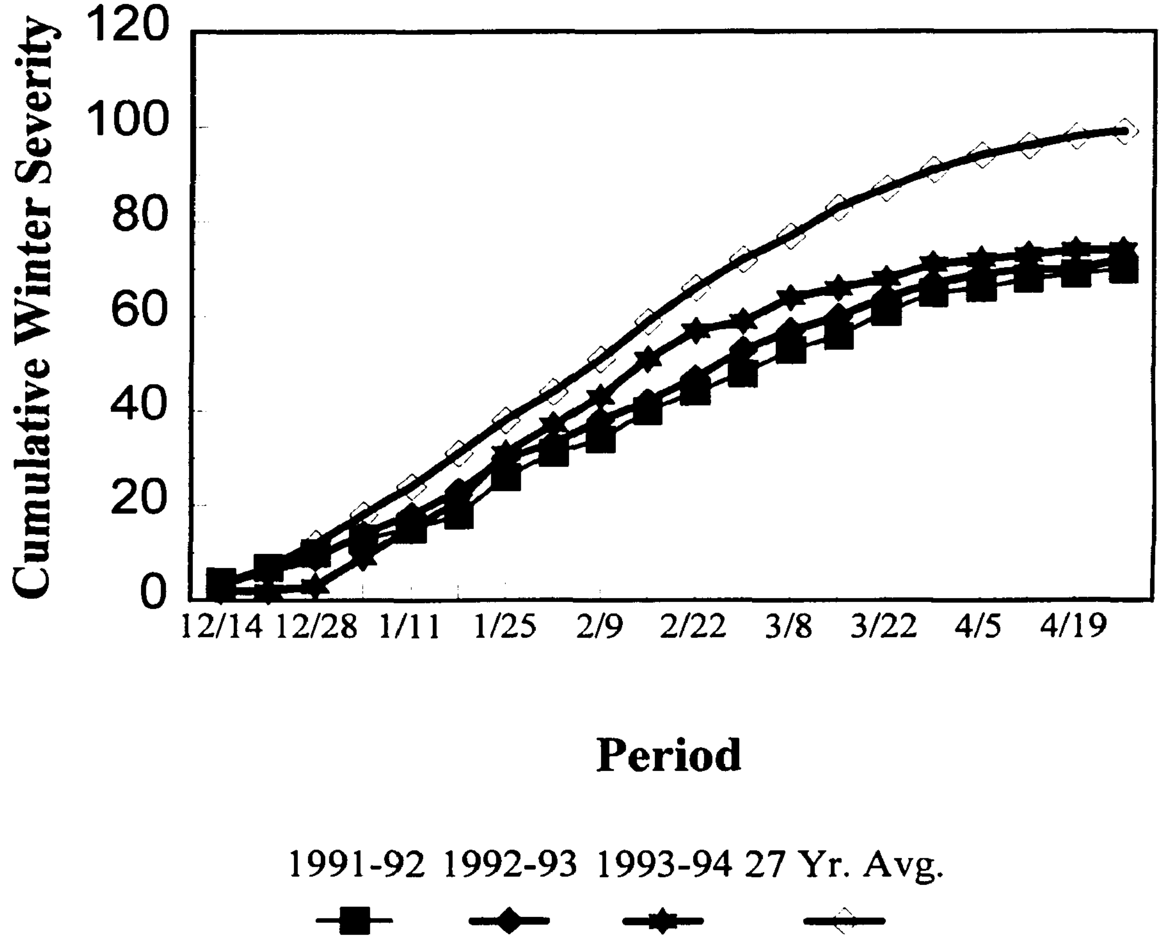


Figure 3. Winter Severity Indices (Verme 1968) for recent winters in the central Upper Peninsula of Michigan relative to the 27-year average.

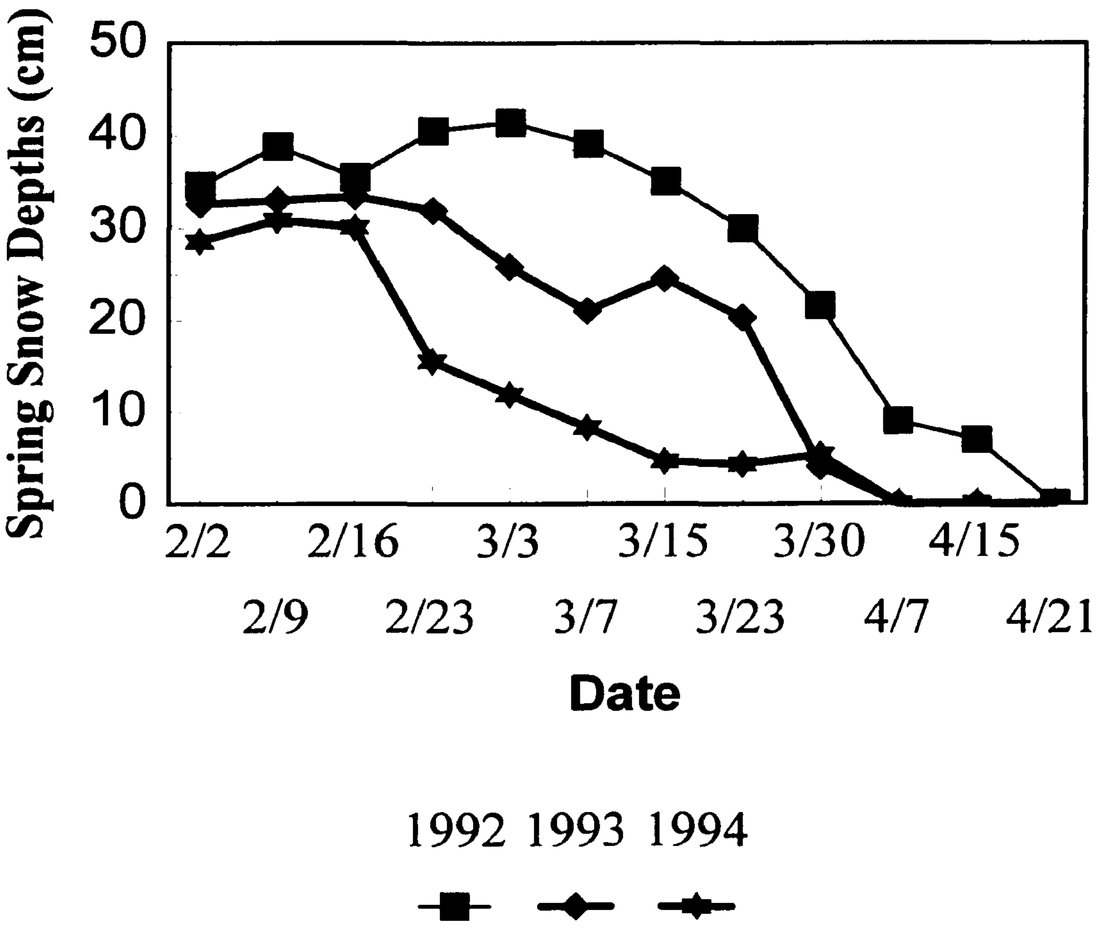


Figure 4. Mean spring snow depths for the the study area during 1992, 1993, and 1994.

Table 3. Mean February Snow depths (MEAN) and first snow free date (DATE) at the 8 snow depth stations along a north - south gradient.

Station	1992 MEAN (cm)	1992 DATE	1993 MEAN (cm)	1993 DATE	1994 MEAN (cm)	1994 DATE
8(north)	52	21 Apr.	43	27 Apr.	35	7 Apr.
7	41	21 Apr.	31	27 Apr.	22	7 Apr.
6	32	21 Apr.	23	27 Apr.	18	7 Apr.
5	27	21 Apr.	19	21 Apr.	18	30 Mar.
4	20	21 Apr.	16	21 Apr.	13	30 Mar.
3	30	21 Apr.	24	21 Apr.	16	30 Mar.
2	22	21 Apr.	16	21 Apr.	18	14 Mar.
1 (south)	19	15 Apr.	15	21 Apr.	19	14 Mar.

The median last day on the winter range was 13 April in 1992 (n = 22, Range = 18 March - 8 May), 29 March in 1993 (n = 28, Range = 25 February - 18 May), and 4 April in 1994 (n = 17, 14 February - 25 April). For the three years combined, the median last date on the winter range was 4 April. A Kolmogrov-Smirnov test suggested that the 1993 dates were from a different parent distribution than 1992 or 1994 ($P < 0.0001$). The difference between 1992 and 1994 was not significant ($P = 0.097$).

The median last day on the summer range was 8 December in 1992 (n = 9, Range = 9 November - 18 January) and 21 December in 1993 (n = 13, Range = 2 November - 28 February). The data for winter 1994 are incomplete because I stopped locating the deer regularly on 20 December 1994. Later locations on 9 and 10 January 1995 indicated several deer still on their summer ranges, suggesting that the winter 1994 migration was relatively late. There was no difference between 1992 and 1993 dates (Mann-Whitney U = 38.5, P = 0.181). The median date for both years combined was 15 December.

Using 4 April and 15 December to delineate time spent on the summer range and winter range for all deer (those that did not show obvious seasonal migrations and those that did), I calculated distances between the harmonic mean centers of the winter ranges and summer ranges. Median distance was 5.51 km in 1992 (n = 38, Range = 0.1 - 54.0 km), 9.19 km in 1993 (n = 50, 0.1 - 51.9 km) and 1.66 km in 1994 (n = 41, Range = 0.1 - 46.0 km). There was no difference with respect to year (Kruskal Wallis statistic [KW] = 3.75, P = 0.150). With the years pooled, there was no difference with respect to age class (KW = 0.623, P = 0.732), sex (U = 1379, P = 0.152), age/sex class (KW = 3.64, P = 0.303), or deeryard (U = 1182, P = 0.671).

Direction was defined as the direction of travel from the harmonic mean center of the winter range to the harmonic mean center of the summer range. The Rayleigh test (Batschelet 1981) indicated that the directions for each year were highly oriented ($P < 0.001$). The mean direction was 26.8° ($n = 38$) in 1992, 25.0° ($n = 50$) in 1993, and 17.7° ($n = 41$) in 1994. Angular deviations (equivalent to standard deviations in linear statistics) were 48.8°, 49.9°, and 61.9° respectively. Data were ranked according to Batschelet (1981) for statistical tests. Directions did not differ between years ($KW = 0.017$, $P = 0.992$). With the years pooled, there was no difference with respect to age ($KW = 1.162$, $P = 0.559$), sex ($U = 1725$, $P = 0.704$) or age/sex class ($KW = 1.408$, $P = 0.704$). Differences with respect to deeryard were insignificant in 1992 ($U = 159$, $P = 0.549$), 1993 ($U = 340$, $P = 0.590$) and 1994 ($U = 242$, $P = 0.388$). Distance and direction of spring migrations are illustrated in Figures 5, 6, and 7.

Median winter range sizes were 212.4 ha in 1992 ($n = 42$, Range = 11.6 - 7331.2), 212.0 ha in 1993 ($n = 51$, Range = 9.1 - 61367.0), and 194.5 ha in 1994 ($n = 49$, Range = 0.2 - 31173.3). Area distributions from each year came from the same parent distributions (Kolmogrov-Smirnov test, $P > 0.626$) and median values did not differ ($KW = 0.398$, $P = 0.820$). With the years pooled, winter range size did not differ with respect to age class ($KW = 4.006$, $P = 0.135$), sex ($U = 2226.5$, $P = 0.681$), or sex/age class ($KW = 3.875$, $P = 0.568$). Winter range areas did not differ between the Stonington and Whitefish deeryards ($U = 2274$, $P = 0.256$).

Median summer ranges were 439.6 ha in 1992 ($n = 37$, Range = 40.8 - 20799.6), 490.3 ha in 1993 ($n = 49$, Range =5.5 - 47017.2), and 170.0 ha in 1994 ($n = 40$, Range =

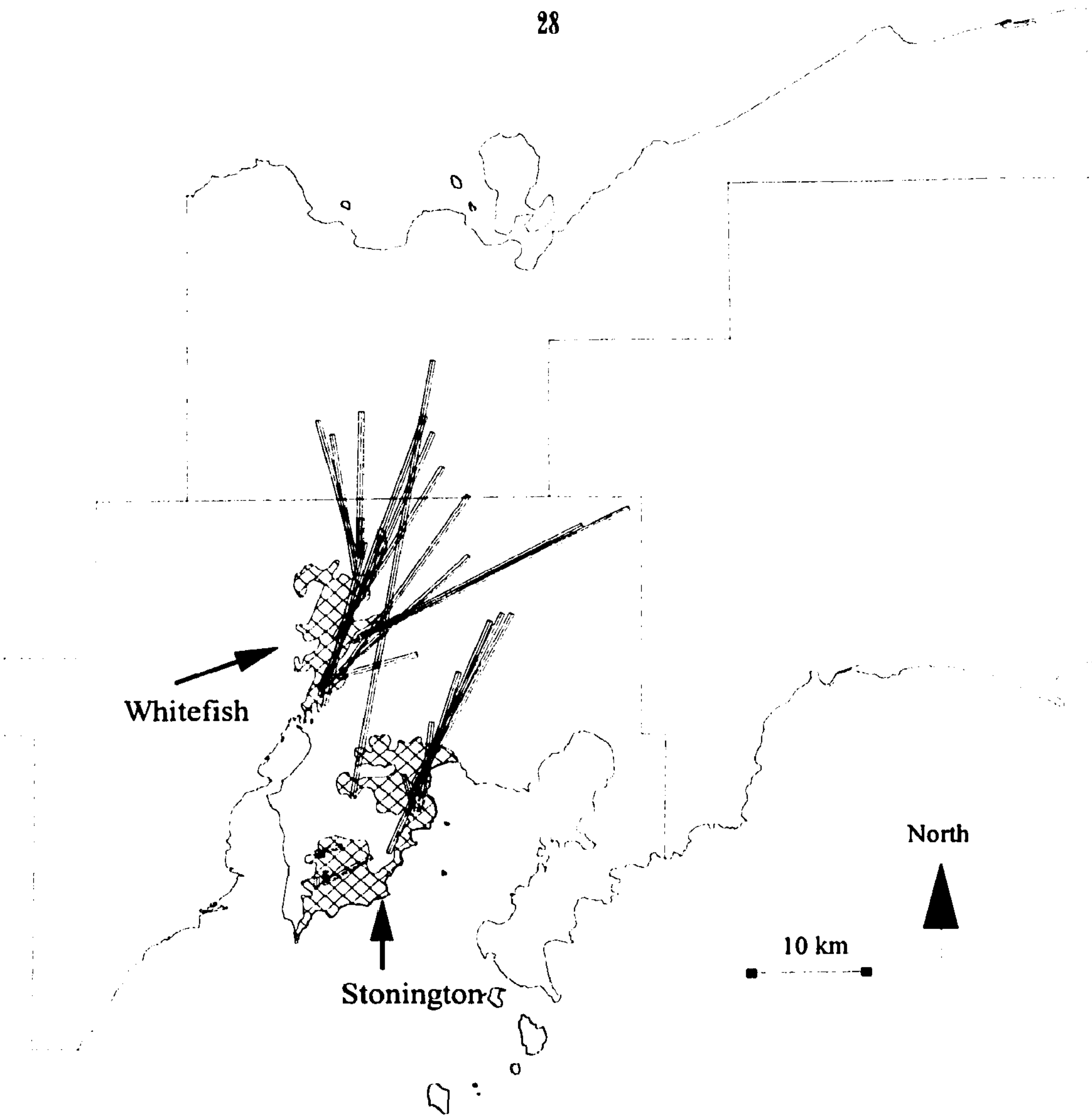


Figure 5. Distance and direction of spring 1992 migrations from the Stonington and Whitefish deeryards.

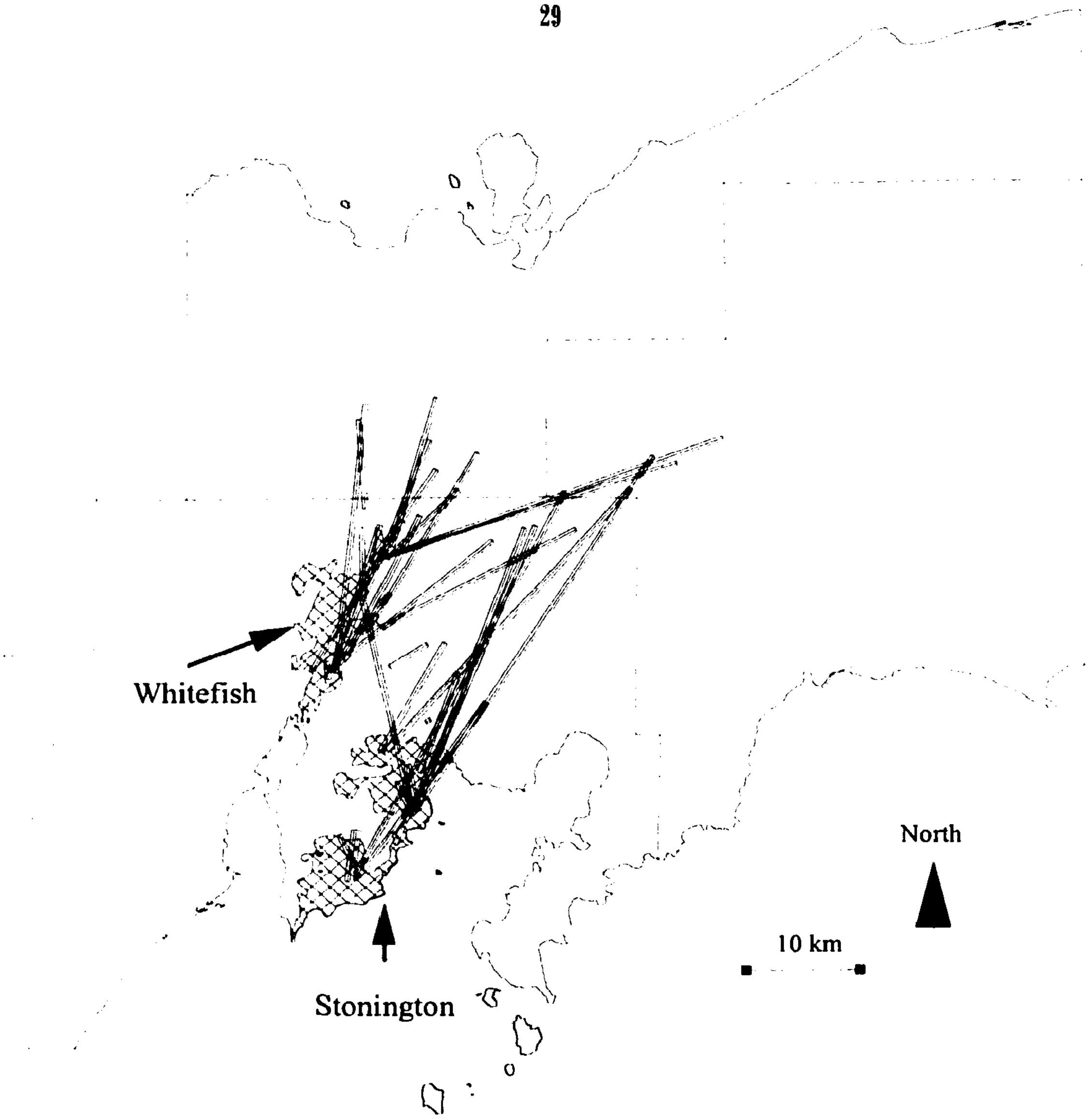


Figure 6. Distance and direction of spring 1993 migrations from the Stonington and Whitefish deeryards.

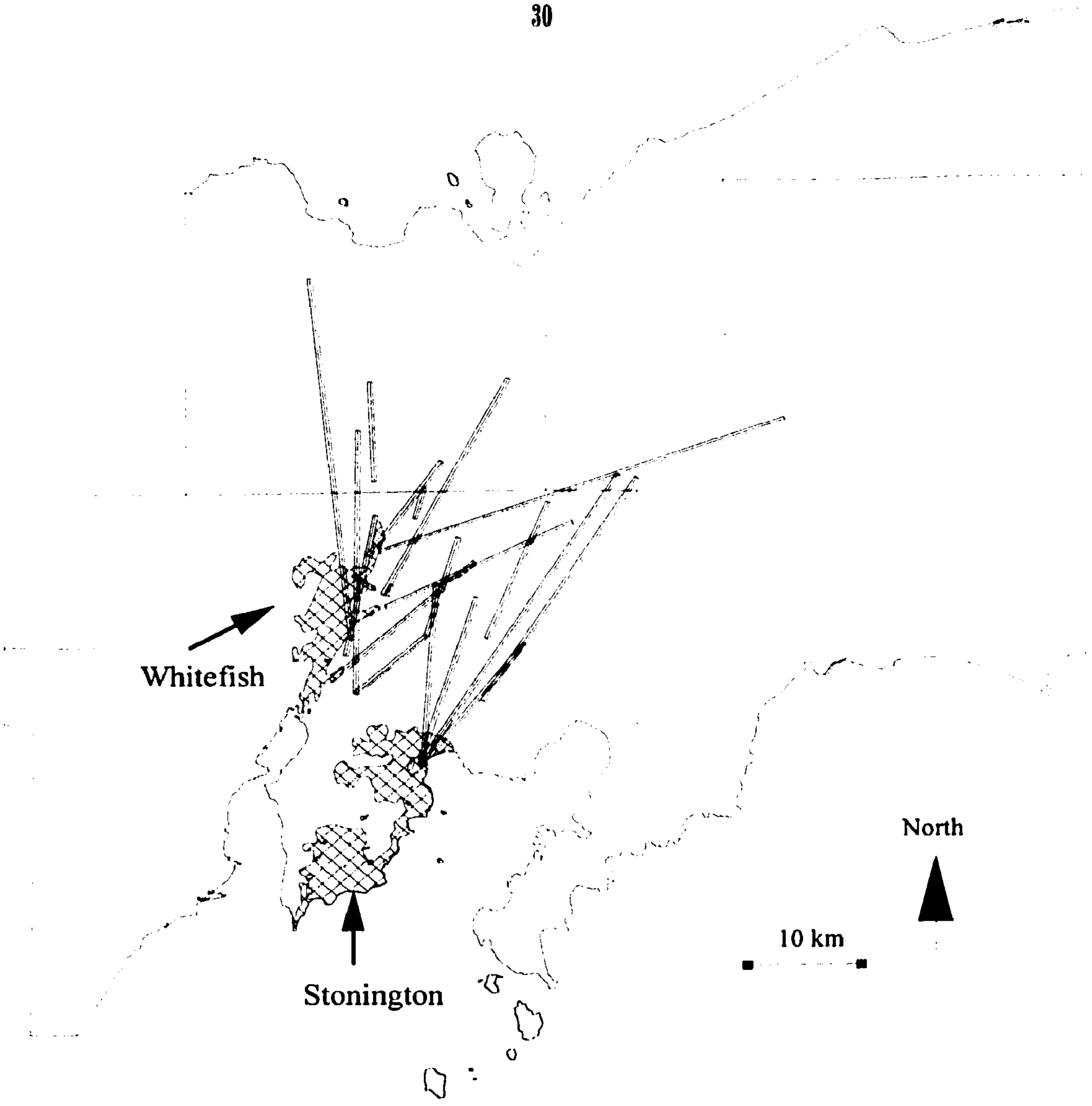


Figure 7. Distance and direction of spring 1994 migrations from the Stonington and Whitefish deeryards.

30.3 - 11759.6). Area medians were different (KW = 6.753, P = 0.034) and the area distribution from 1994 was different from 1992 (P = 0.036) and 1993 (P = 0.030, Kolmogrov-Smirnov test). Summer range area distributions did not differ for 1992 and 1993 (P = 0.817). During 1994, summer range area medians did not differ with respect to age class (KW = 1.271, P = 0.530), sex (U = 166, P = 0.844) or sex/age class (KW = 3.379, P = 0.642). With the 1992 and 1993 summer ranges pooled, summer range area medians did not differ with respect to age class (KW = 3.824, P = 0.148), sex (U = 296, P = 0.108), or age/sex class (KW = 7.99, P = 0.157). Differences with respect to deeryard were significant in 1994 (U = 296, P = 0.006) and in the 1992 - 1993 pooled sample (U = 1218, P = 0.011). In both cases, Whitefish summer ranges had a larger average rank indicating that the summer ranges of Whitefish deer were larger. Assuming a circular shape, the 85th percentile of all summer range diameters (see migration definition) was 6.8 km.

I tested for differences in the size of summer and winter ranges using paired comparisons of summer and winter ranges used by an individual deer each year. In 52 of 125 such pairings the summer range was larger than the winter range. The converse was true in the remaining 73 pairings. A test of the null hypothesis that summer and winter ranges come from the same parent distribution using the Wilcoxon Signed Rank test bordered on significance (P = 0.067).

Incidence of migration among the radio-collared deer is illustrated in Table 4 for migration definition 1 (no overlap) and in Table 5 for definition 2 (separation > 85 percentile of summer range diameters). When stratified for the effects of deeryard, both

Table 4. The incidence of migratory deer when migration is defined by a lack of spatial overlap between summer and winter ranges.

Deeryard	Sex	Migratory	Non-migratory	Ambiguous
Stonington	Male	4	9	0[a]
	Female	10	15	3
Whitefish	Male	11	7	1
	Female	14	7	2

[a] Deer which could be classified differently in different years

Table 5. The incidence of migratory deer when migration is defined by a separation of summer and winter ranges centers greater than 6.8km (the 85th percentile of summer range diameters).

Deeryard	Sex	Migratory	Non-migratory	Ambiguous
Stonington	Male	6	7	0[a]
	Female	8	19	1
Whitefish	Male	9	7	2
	Female	15	6	1

[a] Deer which could be classified differently in different years

sexes were equally likely to be migratory under definition 1 (Mantel-Haenszel test, P = 0.428) and 2 (Mantel-Haenszel test, P = 0.972). When stratified for the effects of sex, Whitefish deer could be considered more migratory under both definitions (Mantel-Haenszel test, P = 0.010, P = 0.010).

Of the 13 deer that could be evaluated for traditional use of winter ranges, 61% were traditional, 23% shifted winter ranges from one year to the next, and 15% showed use of winter ranges that was ambiguous.

Nineteen deer could be evaluated for traditional use of the summer range. Sixteen (84%) were strictly traditional. Two (11%) showed use of the summer range that was ambiguous. One (5%), a yearling male who dispersed, shifted its summer range.

Comparisons of composite seasonal range overlap among the Stonington and Whitefish deer revealed essentially no overlap during the winter (Figures 8 - 10). Summer overlap of the composite ranges was 3% in 1992 (Figure 11) 29% in 1993 (Figure 12) and 38% in 1994 (Figure 13). For each deeryard during each of the three years, composite winter ranges were almost entirely contained within composite summer ranges.

From 1991 to 1994 the Michigan Department of Natural resources compiled 102 reports of Whitefish deer (green ear tags) shot during the hunting season or seen and reported. Nine of the reports were without tag numbers and 31 were duplicate sightings (the same deer seen in the same place) based on reported tag number. Assuming the tag numbers were reported correctly, at least 62 individual deer were seen after having been ear-tagged in the Whitefish yard. One hundred and nine reports were compiled for the

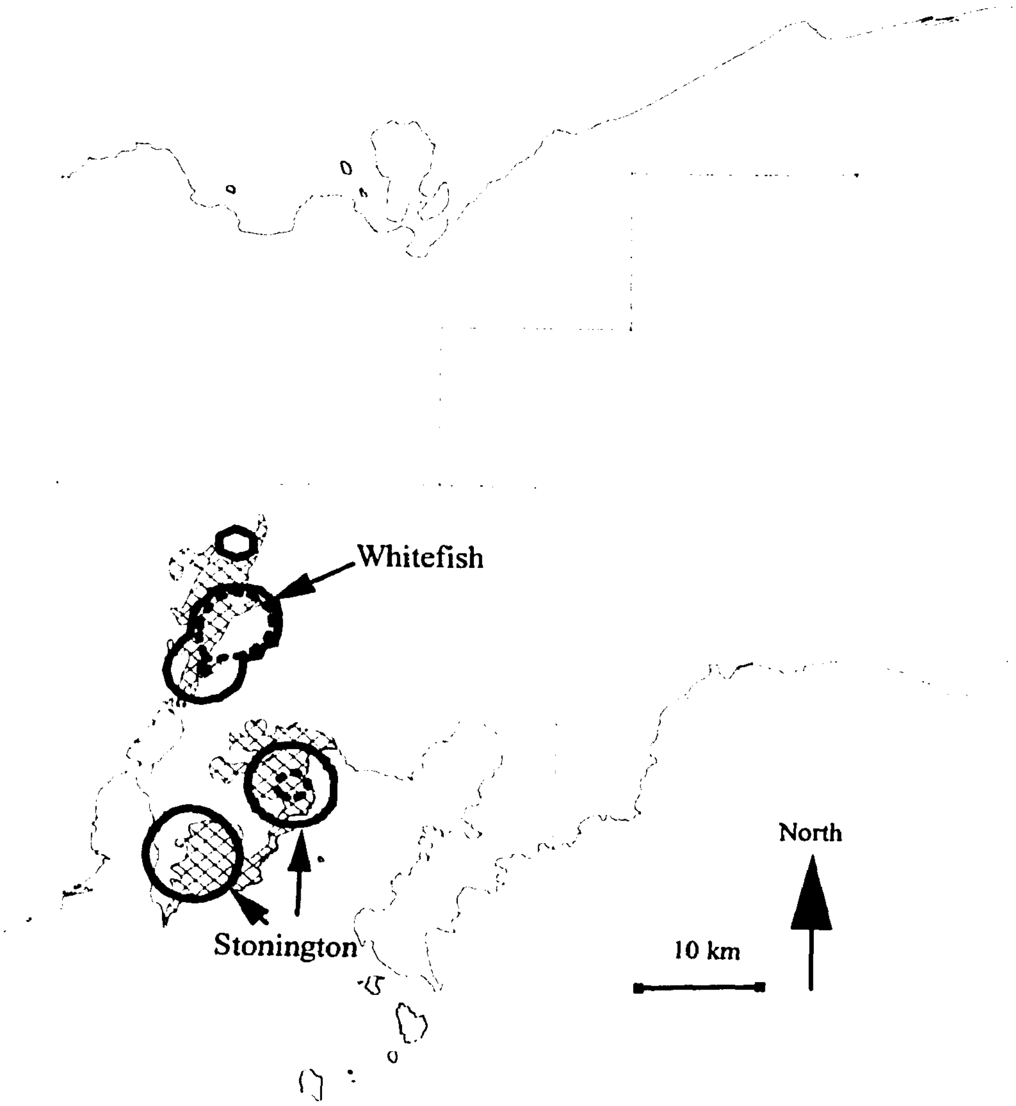


Figure 8. Composite 1992 winter ranges of radio-collared deer using the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

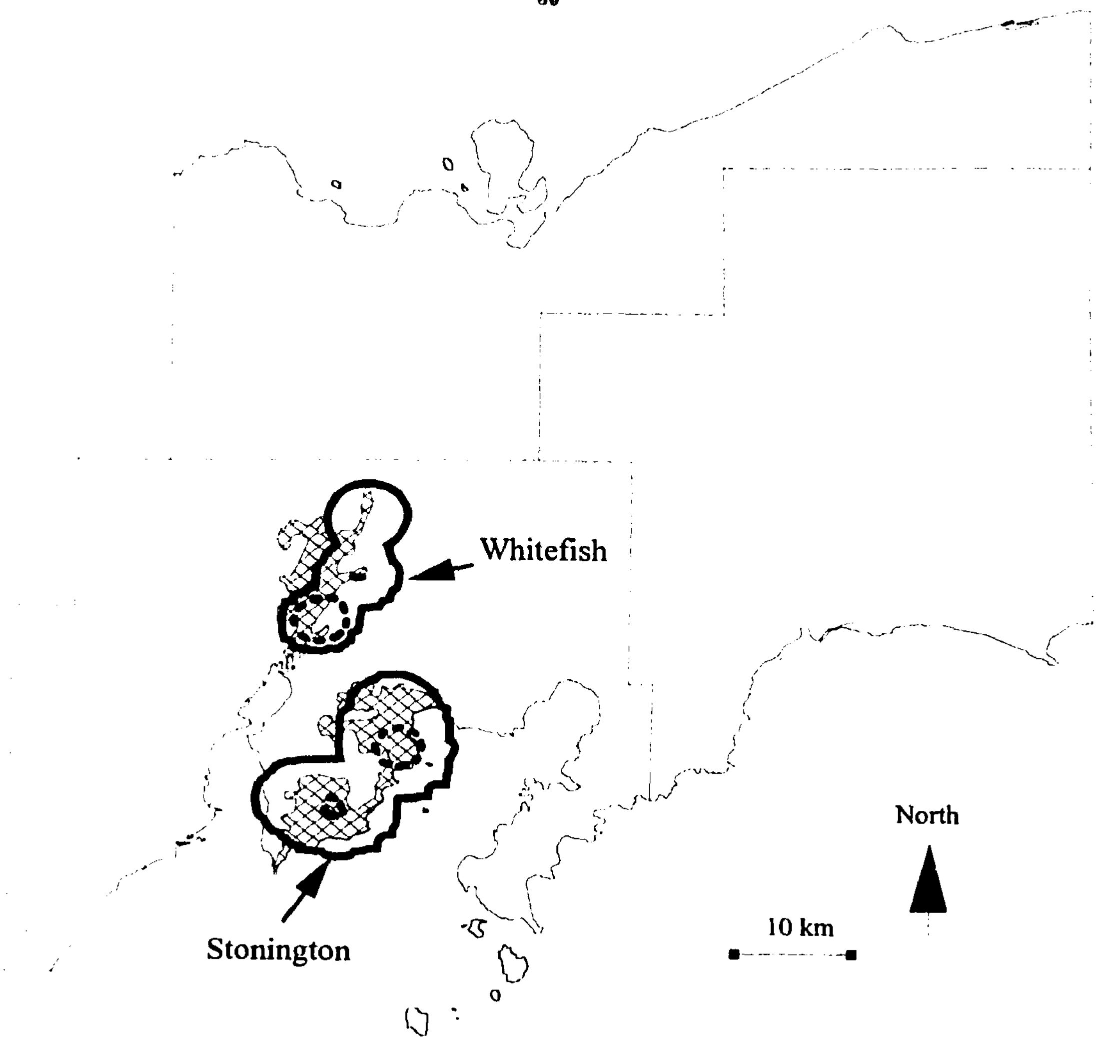


Figure 9. Composite 1993 winter ranges of radio-collared deer using the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

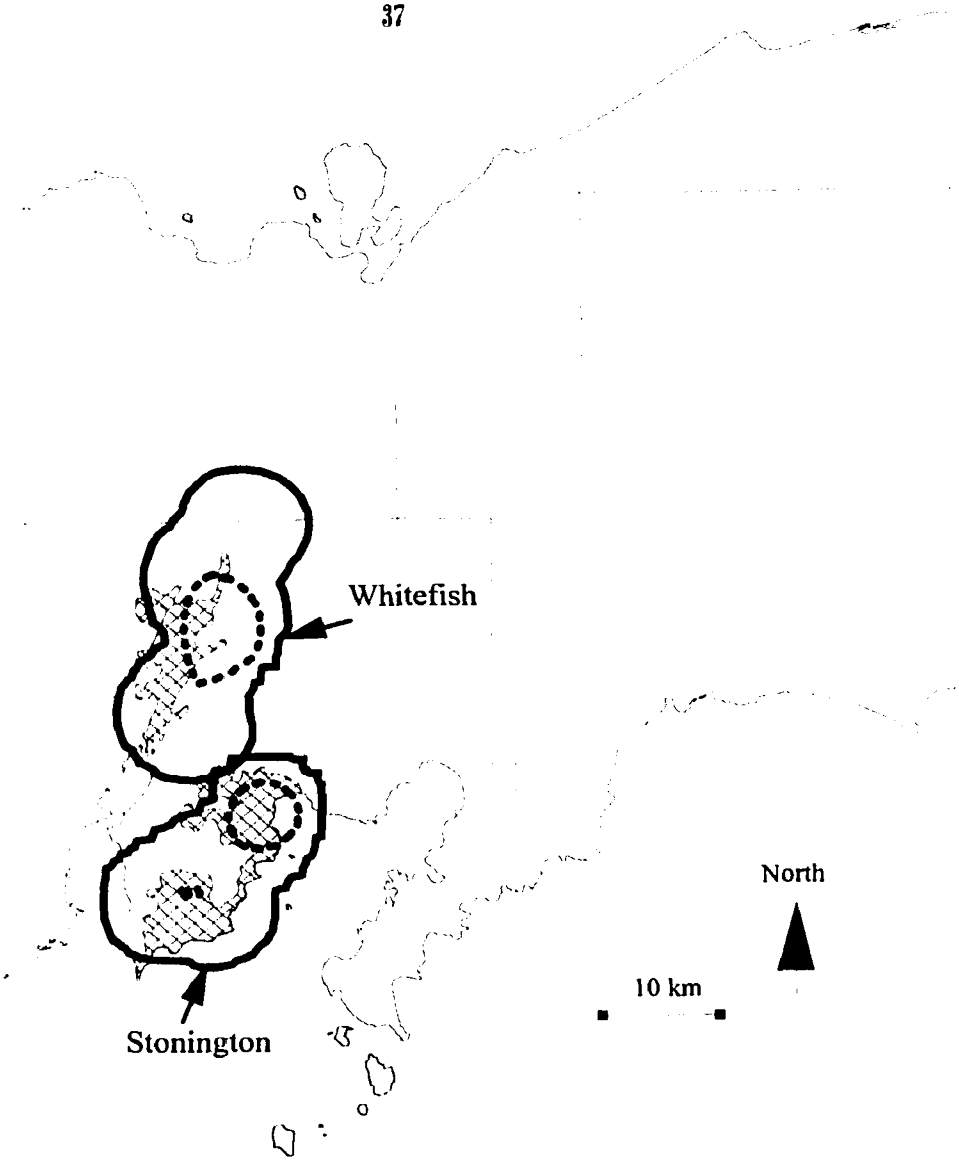


Figure 10. Composite 1994 winter ranges of radio-collared deer using the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

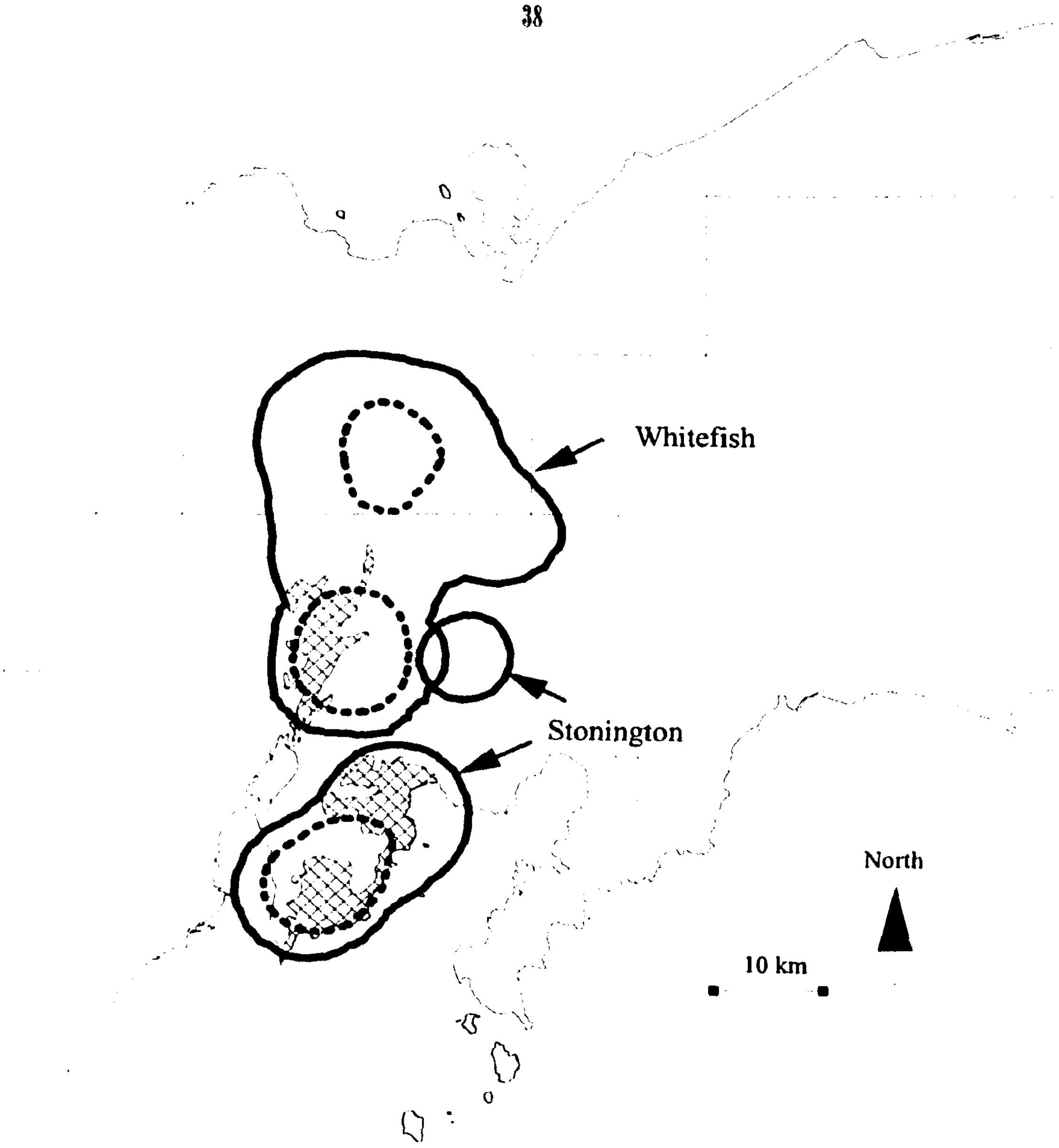


Figure 11. Composite 1992 summer ranges for radio-collared deer that winter on the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

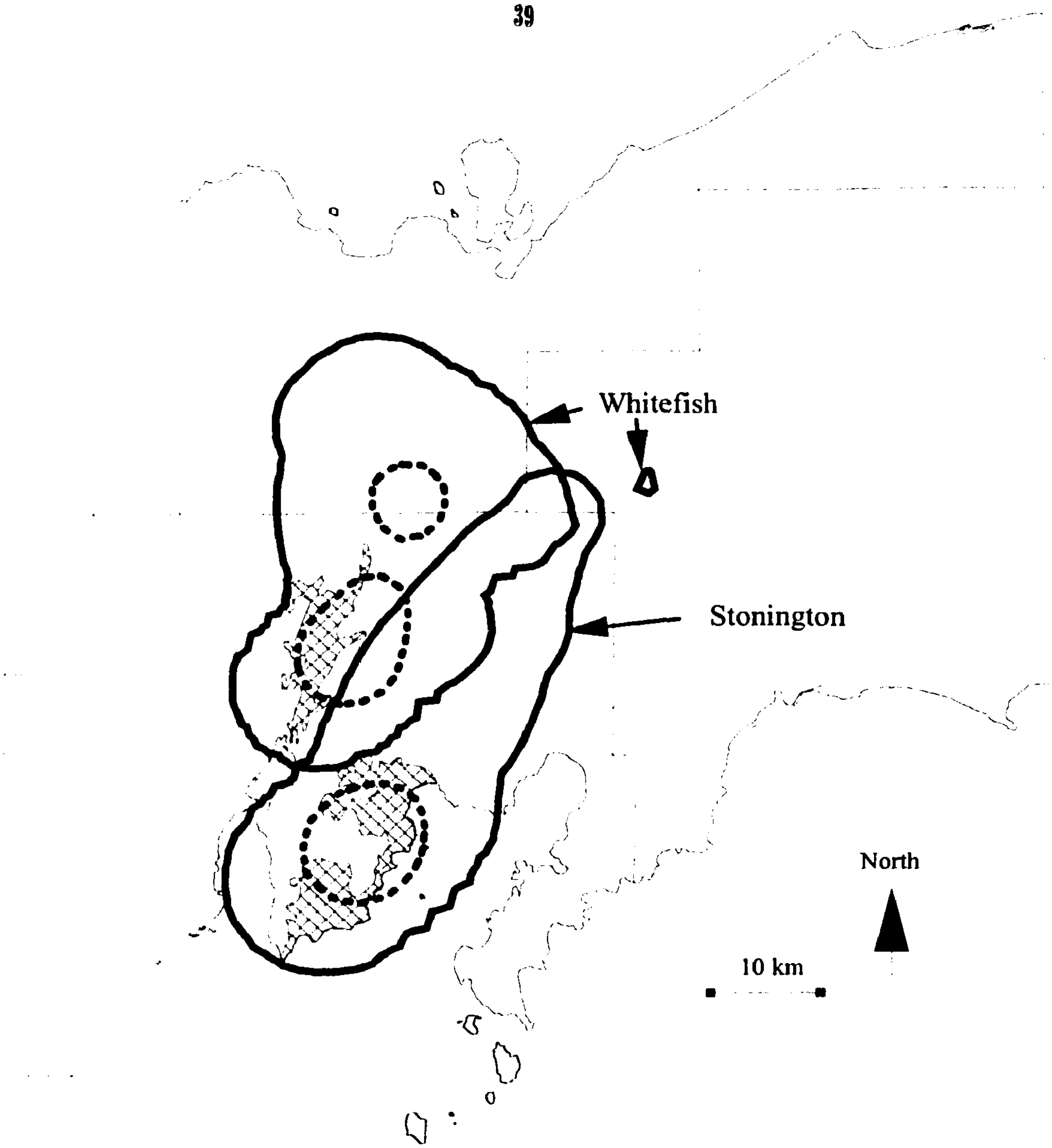


Figure 12. Composite 1993 summer ranges for radio-collared deer that winter on the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

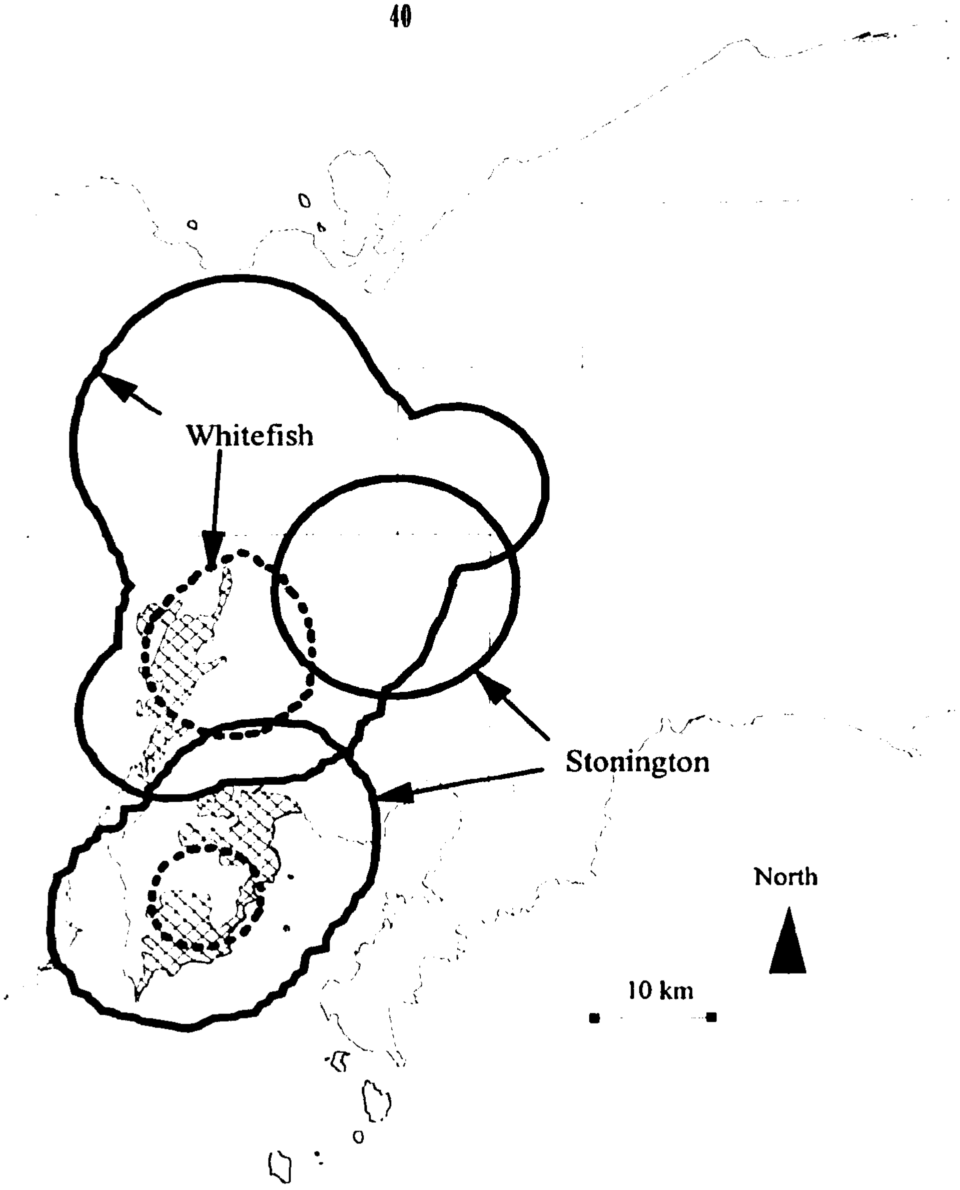


Figure 13. Composite 1994 summer ranges for radio-collared deer that winter on the Stonington and Whitefish deeryards. The 50% (broken lines) and 95% (solid lines) adaptive kernel contours (Worton 1989) are shown.

Stonington deer (blue or orange ear tags) including 23 whose tag number was unknown, and 18 that were duplicates. At least 68 individuals were re-sighted after having been ear-tagged on the Stonington deeryard.

Composite ranges for the reported locations of ear-tagged deer were constructed with duplicate sightings removed so that data points would be independent. Composite summer ranges (all years combined) for the sample of radio-collared deer from the Whitefish deeryard show relatively close agreement with the composite ranges constructed from the reported locations of green ear-tagged deer (Figure 14). Even the bi-lobed 50% contour of the radio-collared deer matched the two discontinuous 50% contours of the sighted deer.

Similarly constructed composite ranges of the Stonington deer did not match as well (Figure 15). The composite range from the ear tag sightings is much larger than that of the radio-collared deer and include a large area west of the deeryard that was not visited by the radio-collared deer.

Estimated deer densities for each year for each deeryard are given in Table 6. T tests within years suggested that deer densities did not differ with respect to deeryard. I suspected that observer bias would cause spurious results, so year to year tests were not performed.

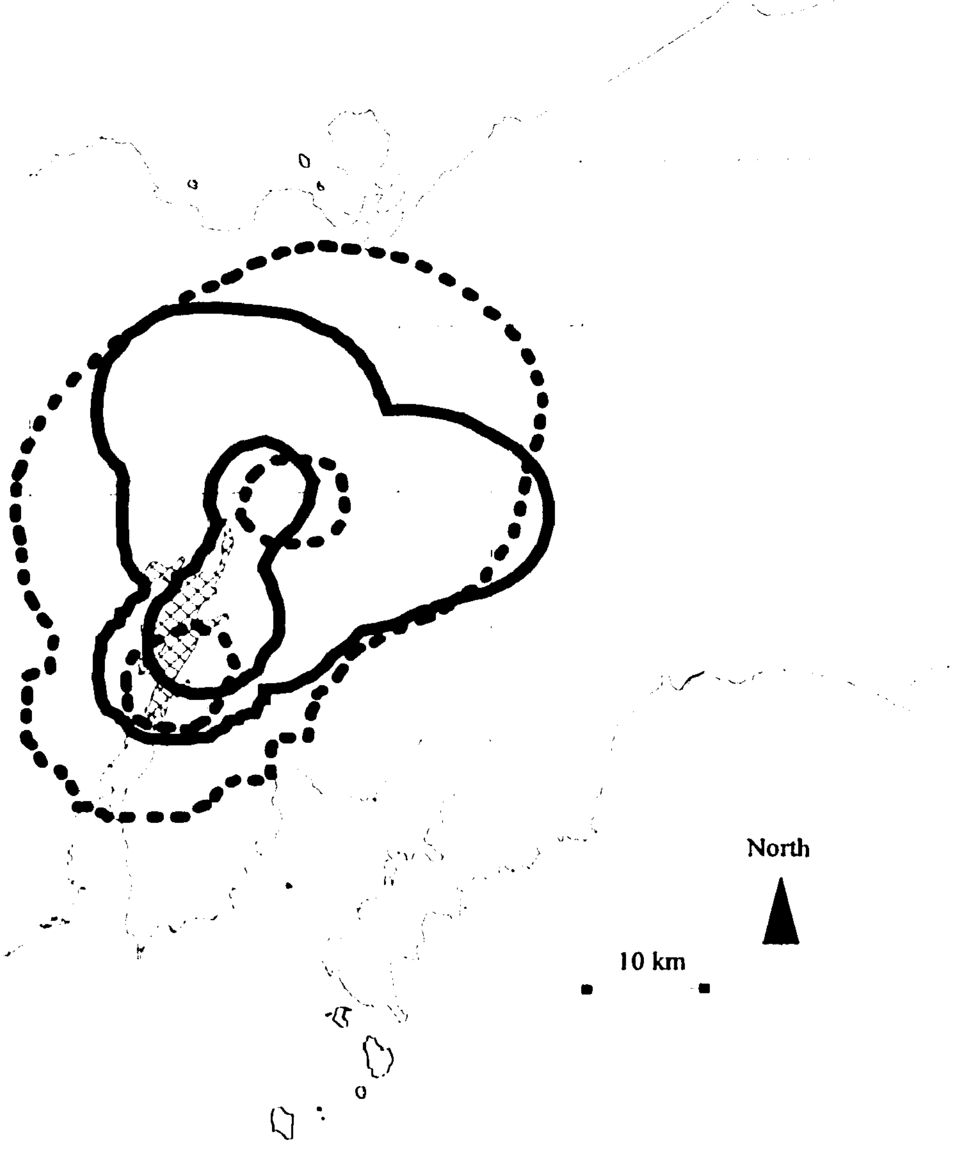


Figure 14. Composite ranges of sightings and kill sites of ear-tagged deer (broken lines) and harmonic mean summer range centers of radio-collared deer (solid lines) that winter in the Whitefish deeryard. The 50% (inner) and 95% (outer) adaptive kernel contours (Worton 1989) are shown.

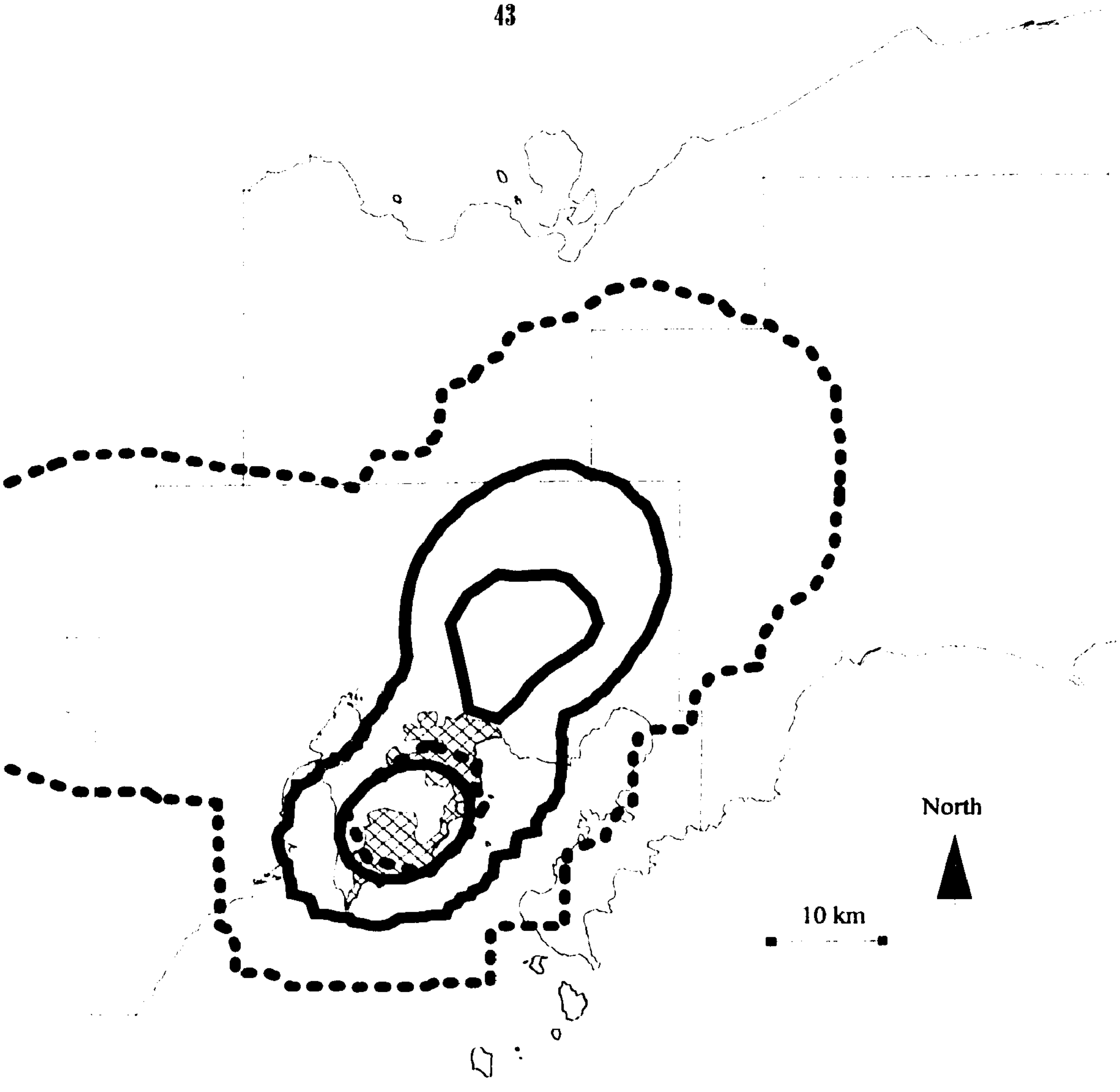


Figure 15. Composite ranges of sightings and kill sites of ear-tagged deer (broken lines) and harmonic mean summer range centers of radio-collared deer (solid lines) that winter in the Stonington deeryard. The 50% (inner) and 95% (outer) adaptive kernel contours (Worton 1989) are shown.

Table 6. Over-winter deer densities for the Stonington and Whitefish deeryards estimated from pellet-group counts.

Year	Deeryard	Deer/km^2	SE
1992	Stonington	65.2	2.4
	Whitefish	52.2	1.5
		t = 1.227	P = 0.223
1993	Stonington	24.6	1.1
	Whitefish	31.7	1.4
		t = -1.050	P = 0.296
1994	Stonington	35.1	1.1
	Whitefish	40.3	1.1
		t = -0.868	P = 0.388

Discussion

TIMING OF SPRING MIGRATION

April and May departure dates for spring migration in this study agree with spring migration dates for studies in Minnesota (Hoskinson and Mech 1976, Nelson and Mech 1981, Nelson 1995), Wisconsin (Hammerstom and Blake 1939, Rongstad and Tester 1969), South Dakota (Sparrowe and Springer 1970), and Illinois (Nixon et al 1991a). Spring migration is associated with warming spring weather (Sparrow and Springer 1970, Verme and Ozoga 1971, Nixon et al. 1991a). Verme (1968) reported that deer began to leave the deeryards when snow disappeared from the adjacent uplands. Snow melt (Hoskinson and Mech 1976, Tierson et al. 1985) and warming temperatures (Drolet 1976) have been frequently suggested as environmental cues (Nelson and Mech 1981). Nelson (1995) analyzed 19 years of spring migration dates in Minnesota encompassing enough climatic variation to separate the confounding effects of temperature and snow depth. He found that mean weekly snow depths in March and mean temperatures in April explained most of the variation in winter range departure dates. Predicted departure dates from his model closely matched departure dates from this study (Nelson 1995). Seasonal range shifts of non-migratory deer on the George Reserve were also associated with snow melt and warming temperatures (Beier and McCullough 1990).

In this study, spring departure dates were earlier in 1993 than in 1992 or 1994. This is unexpected since both the 1993 snow melt pattern (Figure 4) and the 1993 winter severity index (Figure 3) were intermediate to those from 1992 and 1994, although the 30

March snow depth was lowest in 1993. The 1993 anomaly may be a result of variation in the responses to warming trends among the individual radio-collared deer (Nelson 1995). Some northern deer delay spring migration until well after warm temperatures and melting snow have prompted other deer to migrate (Rongstad and Tester 1969, Hoskinson and Mech 1976, Nelson and Mech 1981). Some Illinois deer migrate after leaf out and well after spring temperatures are above freezing (Nixon et al. 1991a, Nixon et al. 1994). Delayed departure dates are associated with quicker spring migration such that most deer arrive on the summer range by May (Hoskinson and Mech 1976, Nelson and Mech 1981), a phenomenon that may be related to plant phenology and parturition timing (Hoskinson and Mech 1976).

TIMING OF FALL MIGRATION

The late November to mid-December departure dates for fall migration agree with studies from Wisconsin (Hammerstrom and Blake 1939) Michigan (Verme 1973), and Minnesota (Hoskinson and Mech 1976), although Minnesota deer begin leaving their summer ranges in as early as late October (Nelson 1995).

The onset of Fall migration is associated with falling temperatures and increasing snow depths (Severinghaus and Cheatum 1956, Telfer 1970, Drolet 1976, Hoskinson and Mech 1976, Nelson 1995). Falling temperatures seem to be the stronger environmental cue (Ozoga and Gysel 1972, Nelson 1995). In a Michigan study, January wind chill first prompted deer to concentrate on the deeryards despite substantial December snow (Verme and Ozoga 1971). Nelson (1995) reported that decreasing temperature alone was a weak stimulus for keeping deer on their winter ranges. Snowfall prior to or concurrent with declining temperatures strengthened the migratory response, suggesting that snowfall had an additive effect. Verme (1973) found that hunter-killed deer were shot closer to their deeryards during colder Novembers, indicating that migration back to the deeryards had begun earlier.

In Minnesota, Fall-migrating deer are more vulnerable to hunters (Nelson and Mech 1981) and wolves (Nelson and Mech 1991), suggesting that predation and hunting mortality may be partially a function of late fall weather conditions (Verme 1973).

WINTER RANGE TO SUMMER RANGE DISTANCES

Winter-summer range distances in this study (Figures 5, 6, 7) were comparable to the movement distances reported for other studies. Recoveries of ear-tagged deer in northern Michigan averaged 9.7 - 14.5 km (max = 40.2 km) in one study (Bartlett 1938), and 13.8 km (max = 51.5 km) in another (Verme 1973). Carlsen and Farmes (1957) reported a median distance of 6.4 km for ear-tag returns for Minnesota deer in coniferous habitat. Rongstad and Tester (1969) reported the recovery of an ear-tagged Minnesota deer 104.6 km from where it was trapped. In South Dakota, tag recovery distances were greater for deer tagged during the winter (2.5 - 212.6 km) than for deer tagged during the summer (2.3 - 37.1 km) (Kernohan et al. 1994).

Telemetry studies found seasonal movements of up to 20 km in Quebec (Drolet 1976), and an average of 14.4 km in South Dakota (Sparrowe and Springer 1970). Seasonal movements of Minnesota deer were 1.6 - 30.7 km in one study (Rongstad and Tester 1969), 10 - 38 km (Hoskinson and Mech 1976) in another, and averaged 17 km (range = 15 - 40 km) in a third (Nelson and Mech 1981).

Discussions of the distance of seasonal migration are complicated by dispersal. In Minnesota, 64% of the males and 20% of the females dispersed as yearlings from their natal ranges. An additional 9% of the males dispersed as 2-year-olds (Nelson 1993). Similar yearling dispersals were reported for Michigan (Ozoga and Verme 1985), Montana (Dusek et al. 1989) and Illinois (Nixon et al. 1991a, 1994). Dispersal occurred on the summer range, coinciding with parturition (Nixon et al. 1991a) or the rut (Ozoga and Verme 1985, Teirson et al. 1985). Reported dispersal distances for radio-tagged yearlings were 4.8 - 9.6 km (Nelson and Mech 1984), 12 km (Nelson and Mech 1987) mean = 19 km and max = 109.8 km (Dusek et al. 1989), 45 - 50 km (Nixon et al. 1991), mean = 11 km and max = 168 km (Nelson 1993), and 0 - 161 km (Nixon et al. 1994). Usually the maximum distances reported from telemetry studies and tag recoveries are for deer whose sex and age class suggest that the movement is a dispersal rather than a migration. For example the longest movement reported for white-tailed deer, 212.6 km (Kernohan et al. 1994), is that of buck that was tagged as a fawn on the winter range and shot the following fall (B. Kernohan pers. commun.).

DIRECTION OF SPRING MIGRATION

Winter to summer range directions were strongly oriented in a northeasterly direction (Figures 5, 6, 7) apparently independent of gross physiological or topographical features. For deer trapped in the southern part of the Stonington deeryard, this may simply reflect the fact that deer do not migrate into Lake Michigan. Similar orientations were reported by Verme (1973), Hoskinson and Mech (1976), and Nelson and Mech (1987). Migration directions among other midwest and western populations in more open habitat are oriented along river systems because of the associated cover (Sparrow and Springer 1970, Dusek et al. 1989, Nixon et al. 1991a, Kernohan et al. 1994). Similarly, migrations in the Adirondacks followed major stream drainages (Tierson et al. 1985). Nelson (1994) studied the movements of translocated deer and reported that memory of distance and direction were more important to migration navigation than topographic cues. Only Rongstad and Tester (1969) reported migration directions that were random, possibly an artifact of sample size (9) or different environmental conditions.

WINTER RANGE SIZE

Comparisons of the seasonal range sizes with other studies are complicated by the use of different home range estimators. The issue is further complicated by the facts that different software packages can generate different sizes for the same estimators and empirical comparisons of the various common estimators have not been published (Larkin and Halkin 1994). Mackey (1995) compared home range estimators for a subset of these data and found that the Harmonic Mean estimator (HM, Dixon and Chapman 1980) and the Adaptive Kernel estimator (AK, Worton 1989) usually gave larger estimates of home range size than the Minimum Convex Polygon (MCP, Mohr 1947).

Median winter range sizes for the 3 years were similar to the winter range sizes estimated for Wisconsin deer (265 - 353 ha [estimator = grid cell counts], Rongstad and Tester 1969). They were larger than those reported for Minnesota deer (MCP = 26.4 ha, Hoskinson and Mech 1976; MCP = 30 ha, Mooty et al. 1987) and New York deer (MCP = 132 - 150 ha, Tierson et al. 1985), but smaller than those reported for South Dakota deer (699 ha [estimator not given], Sparrowe and Springer 1970).

Winter range size is probably determined by deer energetic needs relative to winter severity, and the quality of shelter and browse available in a region (Moen 1976). Drolet (1976) examined grid cell estimates of winter range size in New Brunswick and found that winter ranges were 949 ha during a snow-free winter, 341 ha during an average winter, and 88 ha during a severe winter. Wisconsin deer made fewer forays into adjacent uplands and maintained smaller winter ranges when there was deep snow (Rongstad and Tester 1969). Winter ranges in this study may have been relatively large for northern deer because the winters of 1991-1994 were relatively mild (Figure 3).

The winter ranges of northern deer tend to be smaller than other seasonal ranges however defined (Heezen and Tester 1967, Rongstad and Tester 1969, Sparrowe and Springer 1970, Hoskinson and Mech 1976, Nelson and Mech 1981, 1984, Tierson et al. 1985, Mooty et al 1987). Results of this study agreed, although differences were not significant at alpha = 0.05.

SUMMER RANGE SIZES

Median summer range sizes were generally similar to summer range sizes reported for deer in Minnesota (MCP = 48 - 410 ha, Hoskinson and Mech 1976; MCP = 109 ha, Nelson and Mech 1981), Wisconsin (242 - 1457 ha [estimator = grid cell counts], Rongstad and Tester 1969), South Dakota (699ha [estimator not given], Sparrowe and Springer 1970), New York (MCP = 221 - 233 ha, Tierson et al. 1985), and New Brunswick (266ha [estimator = grid cell counts], Drolet 1976). The maximum values for summer range size in this study are substantially larger because I included movements during the breeding season and movements between interim ranges (Nelson and Mech

1981) in the summer range calculations. Other authors (Nelson and Mech 1981, 1984) did not. Teirson et al. (1985) found that breeding season movements inflated the range dimensions of New York bucks. Nixon et al. (1991a) found that the "breeding ranges" of Illinois bucks were often larger than their summer ranges.

INCIDENCE OF MIGRATION

Not all northern deer were migratory (Hoskinson and Mech 1976). Roughly half of the radio-collared deer in this study were non-migratory (Tables 4, 5). By contrast, Nelson and Mech (1981) reported that only 2 of 28 radio-collared deer in Minnesota remained on the winter range during the summer. In another study, 17% of their radio-collared deer spent the summer on the winter range (Nelson and Mech 1987). The higher incidence of migration among Minnesota deer is probably related to winter range habitat differences. Northern Minnesota deeryards are discrete pockets of dense conifer cover (M. Nelson pers. commun.). By contrast, the deeryards in southern Delta County are more interspersed with upland and early-seral types.

A different but related phenomenon is that of deer who are "conditional migrators" (Nelson 1994) because they do not leave the summer range during mild winters (Rongstad and Tester 1969, Drolet 1976, Nelson and Mech 1991, Nixon et al. 1991a). During relatively mild winters (such as we had during this study) the relative proportion of non-migratory deer on the winter range may increase because the conditional migrators remain on the summer range. Hence the proportion of non-migratory deer in the radio-collared sample may be inflated because all deer were trapped on the winter range.

DIFFERENCES BETWEEN WHITEFISH AND STONINGTON DEER

Whitefish deer had larger summer ranges and were more likely to be migratory. This was probably because the Whitefish deeryard is located farther north. In the central upper peninsula, snow depth increases south to north (Table 3, Berndt 1977). and deer density decreases south to north (Ozoga et al. 1994). On the average, Whitefish deer occupied less-densely stocked summer habitat where range size may be larger because of fewer agonistic social interactions and wider breeding season movements. Higher snow depths may make it more imperative for deer to migrate.

MIGRATION TRADITION

Even with a fairly restrictive definition for tradition, use of seasonal ranges by deer in this study was very traditional. Traditional use of the same seasonal ranges from year to year is commonly reported in migratory northern deer (Bartlett 1932, 1938, Hammerstrom and Blake 1939, Severinghaus and Cheatum 1956, Rongstad and Tester 1969, Verme 1965, 1973, Nelson and Mech 1981, 1984, 1987, Ozoga et al. 1982, Messier and Barrette 1985, Tierson et al. 1985, Nelson 1995). Traditional use of seasonal ranges is probably an extension of the site fidelity seen in midwestern populations where true migrations are less common or non-existent (Sparrowe and Springer 1970, Beier and McCullough 1990, Nixon et al. 1991a).

Fidelity to summer ranges was stronger than fidelity to winter ranges (Tierson et al. 1985, Dusek et al. 1989, Nixon et al. 1991a, 1994) indicating the possible presence of conditional migrators. Drolet (1976) indicated that traditional use of winter ranges was flexible enough to respond to yearly differences in winter severity. At least 2 of the radio-collared deer wintered near active timber cuttings that were located between their summer and winter ranges. Verme (1973) and Tierson et al. (1985) reported a similar response to winter logging.

Nelson and Mech (1981) reported that the use of intermediate ranges was traditional as well. In this study, doe g141 left the Whitefish deeryard in March moving southeast to an intermediate range where it remained until April or May before migrating to a summer range to the northeast. It repeated this pattern for 3 years in a row. Use of intermediate ranges was associated with longer migrations and may be a way of avoiding the possibility of being caught in late spring storms far away from the deeryards (Nelson and Mech 1981).

MIGRATION AND SOCIAL STRUCTURE

Distance and direction of seasonal movements, and winter and summer range sizes were independent of sex or age class. Similarly, there was no difference with respect to sex in South Dakota (Sparrowe and Springer 1970) or New York (Tierson et al. 1985) home range sizes. In contrast, the parturition ranges of Illinois does increased with age and bucks had larger total home ranges (Nixon et al. 1991b). Home ranges of Colombian white-tailed bucks also increased with age (Gavin et al. 1984). George Reserve bucks (Beier and McCullough 1990) and Minnesota bucks had larger summer ranges (Rongstad and Tester 1969) because of rutting movements (Nelson and Mech 1981, 1984). Females were relatively sedentary (Nelson and Mech 1984). Beier and McCullough (1990) speculated that equivalent summer range sizes could result when highly skewed sex ratios force females to search larger areas for access to mates.

Yearlings in Minnesota had large ranges as well (Nelson and Mech 1981), probably because of dispersal or pre-dispersal movements. Nixon et al. (1994) reported that yearling male home ranges increased substantially following dispersal.

The lack of age-specific differences in migration characteristics fits what is known about the social structure of deer. The functional units of deer society are small groups of related does and their fawns, and looser small groups of unrelated juvenile and adult males (Severinghaus and Cheatum 1956, Hawkins and Klimstra 1970, Hirth 1977). These social groups migrate together (Nelson and Mech 1981) and show fidelity to and often exclusive use of seasonal ranges (Tierson et al. 1985). Migration tradition is maintained though social interactions. Fawns and yearlings learn the migration traditions of their social groups and remain faithful to them throughout life (Nelson and Mech 1981, 1984, Nixon et al. 1991a).

A disruption of social ties may partially explain a high incidence of non-migratory deer. Under intense hunting pressure, more deer are orphaned before they can be taught migration routes resulting in more poorly-developed, population-wide tradition (Larson et al. 1978, Nelson 1994). Nixon et al. (1991a) recognized the value of refugia in allowing deer to live long enough for migration tradition to develop. Holzenbien and Marchington (1992) reported that orphaned buck fawns were less likely to disperse than non-orphans. A series of mild winters may result in a breakdown of migration tradition as well because the fawns of conditional migrators may never be taught to migrate.

The lack of sex-specific differences in migration characteristics is surprising since the sexes maintain exclusive social groups and there are few social interactions between the sexes apart from the breeding season (Hirth 1977). Bucks and does confined to the George Reserve used different vegetation types on the summer range (Beier 1987, Beier and McCullough 1990). Nelson and Mech (1984) reported that the formation of migration tradition in young bucks may extend over a 2 to 3 year period with young bucks occasionally visiting their natal ranges and re-associating with their mothers. This behavior might provide a mechanism for coordinating migration tradition among the sexes' different social groups.

Northern deer appear to have evolved a secondary level of social organization that is tied to the location of suitable winter range in the landscape (Figures 8-13). Nelson and Mech (1987) noted that 95% of their radio-collared deer used summer ranges clearly within the same regions as did other deer from the same deeryard.

During the winter, the primary social groupings coalesce and new social patterns develop (Hoskinson and Mech 1976, Teirson et al. 1985, Nixon et al. 1991a) - probably because of an energetic advantage to avoid fighting (Ozoga 1972). A plastic social structure allows deer to adapt to changing habitat conditions (Hirth 1977). The ability to tolerate social crowding on the deeryards also make deer less vulnerable to coyote (Messier and Barrette 1985) and wolf (Hoskinson and Mech 1976, Nelson and Mech 1981, 1991) predation. In fact, predation may have shaped the patterns of behavior and landscape scale use of deeryards and summer ranges that facilitate traditional migration (Hoskinson and Mech 1976, Nelson and Mech 1981, 1991, Messier and Barrett 1985).

Hawkins and Klimstra (1970), referring to the primary social organization, wrote that deer do not move in herds. Sparrowe and Springer (1970) used the term "herds" to describe larger groups of deer that winter in discrete wintering areas (secondary social organization). In this study, deer that wintered in the Whitefish and Stonington deeryards constituted separate herds (in sensu. Sparrowe and Springer 1970). The herds' territories have little or no overlap on the winter range although overlap on the summer range can be fairly substantial (Figures 12, 13). Summer range territories in Minnesota showed minimal (5%) overlap (Nelson and Mech 1987). Verme (1973), in a trap-tag-release study, also found little evidence of range overlap. The degree of overlap probably depends on deer density and the proximity of deeryards to one another in the landscape.

Nelson and Mech (1987) have suggested that herds of deer that use separate deeryards may fit the definition of a genetic deme (Shields 1987). Since breeding takes place on the summer range, their suggestion may or may not be true. In landscapes where deeryards are infrequent (ie Minnesota [Nelson and Mech 1987]) herds may represent genetically isolated sub-populations (demes). In landscapes where deeryards are more abundant and summer range overlap of separate herds is high, there is likely to be substantial genetic exchange during the breeding season. Even in the absence of genetic arguments, contiguous units of deer populations can have different demographic patterns and operate independently of each other (Dapson et al. 1979).

In this study, composite summer ranges completely overlapped composite winter range for the herd using the different deeryards (Figures 11,12,13). Sparrowe and Springer (1970) described a similar South Dakota population as "partially migratory" because it used all the study area during the summer but withdrew to a small portion during the winter.

DEERYARD DEER DENSITIES

Estimated deeryard deer densities in 1993 and 1994 (Table 6.) were similar to densities reported for other deeryards. Densities in 1992 were relatively high. Deeryard densities were 17 - 18 /km^2 in Quebec (Potvin and Hout 1983, Messier and Barrette 1985), 30 - 40 /km^2 in Wisconsin (Larson et al.1978), 16 - 39 and 3 - 11 /km^2 in Minnesota (Nelson and Mech 1981, Fuller 1991), and 52 and 8 - 25 /km^2 in Michigan (Bookhout 1965, Doepker and Ozoga 1990). Estimates of deer density from pellet-group plots may be severely affected by sample design, environmental factors, variations in deposition rates, and observer bias (Neff 1968, Rogers 1987, Fuller 1990). Year to year differences in density estimates in this study are probably an artifact of observer bias since different personnel assisted in the pellet-group surveys each year. There is no other evidence for the 50% reduction in the size of the deer herds that is implied by the changes in density estimates from 1992 to 1993.

Management Implications

Migration behavior is strongly ingrained in northern deer (Severinghaus and Cheatum 1956, Verme 1973, Teirson et al. 1985). Distance, direction, and seasonal range use are traditional and predictable from year to year. Migration timing and the incidence of migration in conditional migrators is related to weather and may be predictable as well (Nelson 1995).

Individual deeryards supply deer to large portions of the surrounding summer range via spring migrations (Verme 1973). Deer populations depend on the sheltering qualities of deeryards to cope with the severe northern winters. Summer range distributions therefore depend on the deeryard conditions in areas that may be as far away as 50km. Deeryard densities and the patterns of migration might be used to estimate the numbers of deer that a given deeryard supply to the summer range. Caution is warranted because point estimates of deer density from pellet group counts may be unreliable (Fuller 1991).

Trap-tag-release programs appear to be a viable means for managers to map out the summer ranges of deer herds that use discrete deeryards. Care should be taken to eliminate the biases inherent in home range estimators, especially those caused by extreme outliers (which may be dispersals) and non-independent sightings. Bias can be identified if visible numbered ear tags are used and records of age and sex class are kept. Unfortunately the dates associated with the sighting data in this study were unusable. Had I been able to identify duplicate observations in constructing composite ranges for the tag-reported data, the Stonington ranges would probably have been a better match.

Heavy browsing in and around some deeryards may be preventing the regeneration of commercial timber species and impacting forest plant diversity (Bartlett 1938, Jenkins and Bartlett 1959, Habeck 1960, Anderson and Loucks 1979, Verme and Johnson 1986, Alverson et al. 1988, Miller 1990, Pregitzer 1990). Miller (1990) and Mackey (1995) have suggested managers take advantage of the deer's attraction to harvest activity and early seral vegetation. They recommended that managers draw deer from impacted areas by scheduling harvests elsewhere.

This is an untenable management option for two reasons. First, while yarded deer will move into active timber cuttings to feed on the tops and slash (Verme 1965, 1973, Tierson et al. 1985), migration tradition is probably strong enough to preclude the abandonment of one yard for another. Verme (1973) and Nelson and Mech (1981) reported that deer continue to use marginal winter ranges while nearby high quality winter ranges go unused. Verme (1973) found no evidence that deer would shift from one deeryard to another and speculated that the elimination of the entire herd from one yard is likely to leave a large "hole" in the surrounding summer distribution where that herd's traditional summer range was located. Second, given the reproductive (Harder 1980) and dispersal (Nelson 1993) capabilities of northern deer, favored yarding areas are likely to be quickly recolonized before the 20 years or so that it takes to regenerate a cedar or hemlock stand. Presumably, "holes" in the summer range distribution would fill in for the same reasons.

A similar suggestion is that winter cutting can be used to provide yarded deer with enough food such that browsing pressure is reduced enough to allow seedling recruitment. The population response to increased winter food is likely to be increased fawn survival and recruitment (Verme and Ozoga 1971, Moen 1978). This, coupled with migration tradition, suggests that the next year's winter density will be even higher, exacerbating the problem.

Paired summer and winter ranges or groups of paired summer and winter ranges should provide the basis for designating biologically meaningful deer management units (Sparrowe and Springer 1970, Verme 1973, Drolet 1976). I would advocate redrawing Upper Peninsula management units so that boundaries do not separate important deeryards from their summer ranges. Designating deer management boundaries in this fashion would insure that the effects of a different harvest regime in one unit would not be felt primarily in another unit. Figures 16 and 17 illustrate this approach for the study area.

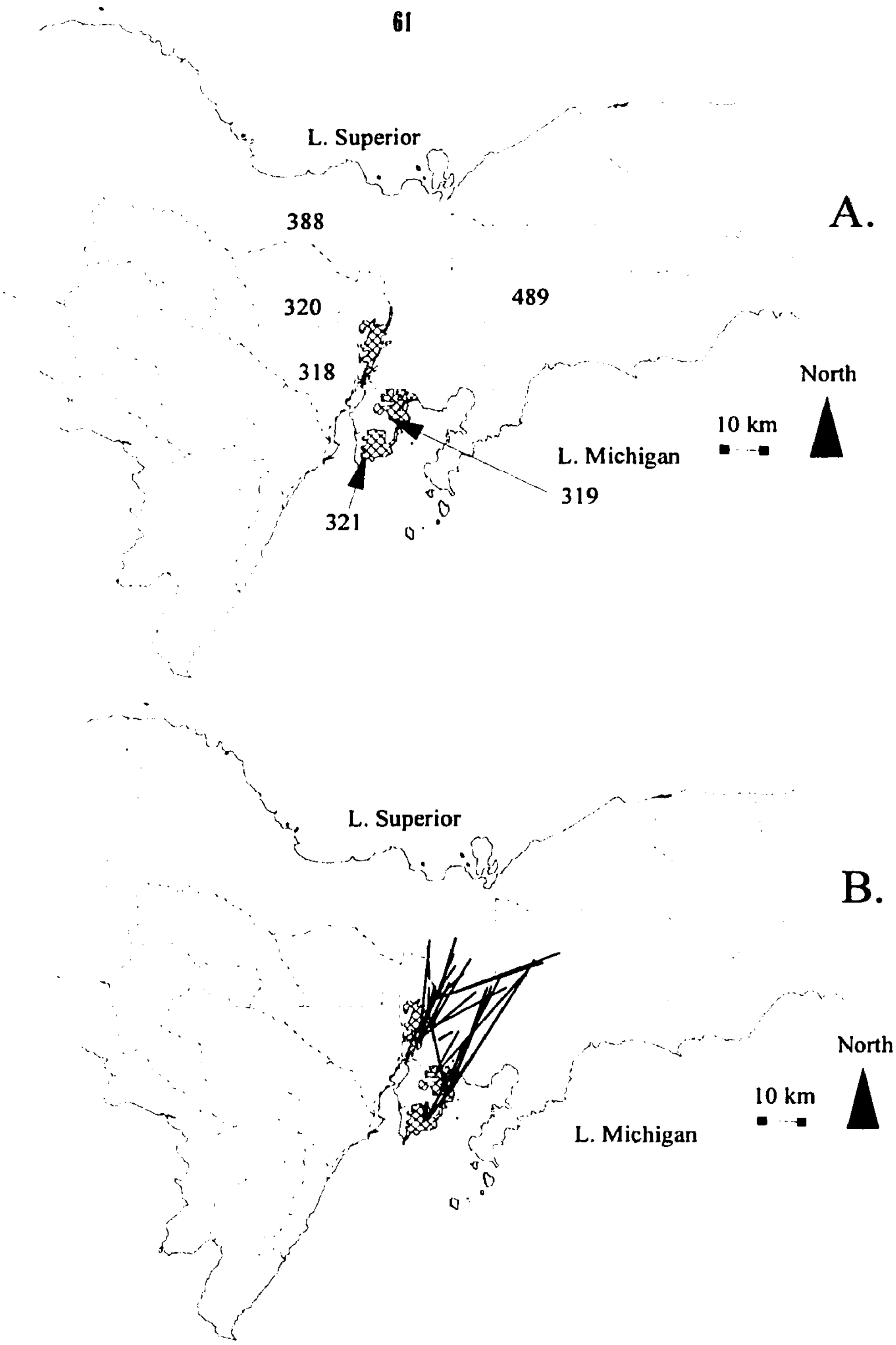


Figure 16. Study area deeryards in relation to deer management units (DMUs, A) and deer migrations (B). Deeryards are contained in DMUs 319, 320, and 321. Spring migrations suggest that corresponding summer ranges are in DMUs 388 and 489..

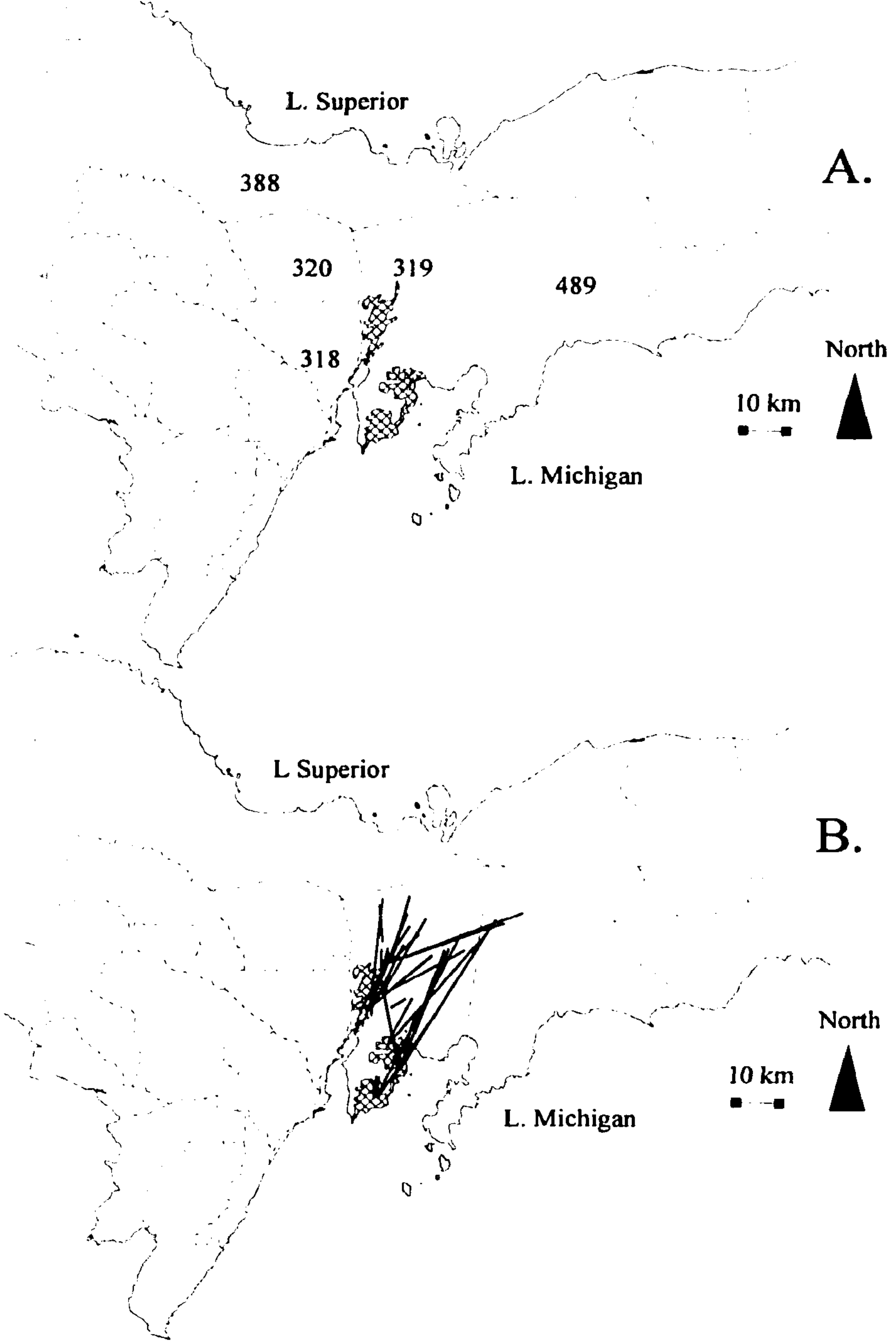


Figure 17. Hypothetical re-drawing of deer management units in the central Upper Peninsula (A.) such that the study area deeryards and their corresponding summer ranges (B.) are kept together.

Chapter 2. Mortality, Age Structure, and Population Genetics of White-tailed deer in Michigan's Upper Peninsula

Mortality, especially non-hunting mortality can be especially variable in northern deer because of varying winter severities from year to year. Specific causes of deer mortality in the Upper Great Lakes include natural predation, domestic dog (Canis familiaris) predation, hunting, poaching, wounding during the hunting season, malnutrition, drowning, road-kills, and other accidental deaths (Blouch 1984, Nelson and Mech 1986b, Fuller 1990). In most populations, mortality related to hunting is highest, and can have a profound effect on the age and sex structure of local populations (Ozoga and Verme 1985, Dusek et al. 1989, 1992, Fuller 1990, Nixon et al. 1991a, 1991b, 1994). Hunting mortality is most important from a management perspective because it is the area of deer population dymanics that is most directly under the manager's control (Fuller 1990). Research on other mortality factors is technically difficult and expensive. Thus, non-hunting mortality is a major unknown in the ecology of white-tailed deer (Halls 1984, DeYoung 1989b).

Michigan, like most states collects information on the sex and age structure of harvested deer each year. Mortality rates can be calculated from the age at death of a sample if a stable age distribution is assumed (Caughley 1966, 1977). Unfortunately, annual deer mortality in northern Michigan fluctuates with winter severity (Verme 1968). This is especially true for fawns, making a stable age distribution unlikely. Moreover, deer harvest data are known to be biased relative to different sex and age classes (Roseberry and Klimstra 1974, Woolf and Harder 1979, Coe et al. 1980, Dusek et al. 1989) and dead deer surveys and population reconstruction techniques provide unreliable mortality information (Woolf and Harder 1979). Direct estimation of survival using radio-telemetry entails fewer assumptions than most other methods, and entails a more detailed assessment of the extent, timing, and causes of mortality (Heisey and Fuller 1985, White et al. 1987, Fuller 1990).

White-tailed deer have a matrilineal social structure with operative units consisting of does, their daughters, and fawns (Nelson and Mech 1981, Ozoga et al. 1982, Marchington and Hirth 1984, Nixon et al. 1991a). Males form bachelor groups in which age determines dominance patterns and access to females during the rut (Hirth 1977, Verme and Ullrey 1984, Marchington and Hirth 1984, Nixon et al. 1994).

In northern regions, severe winters cause deer to seek out specialized habitats where social structure contributes to overwinter survival. In the upper Great Lakes region these specialized habitats are typically mixed-conifer or northern white cedar swamps. Use of these "deeryards" by social groups is traditional and deer migrate between the same winter and summer ranges from year to year (Verme 1973, Chapter 1). Range location for individual deer depend on social bonds and area affinities developed when the deer are young. Typically, yearling males disperse to seek out new ranges different from those of their mothers (Nelson and Mech 1981).

Nelson and Mech (1987) suggested that groups of deer traditionally using separate deeryards represent genetically distinct subunits of the larger population (demes). Genetic differences between sympatric sub-populations on the Savanna River Plant in Georgia suggested that deer populations should be viewed as an aggregation of relatively small sub-populations that vary significantly in allele frequencies over relatively short distances (10 km) and short time periods (3 yrs) (Smith et al.1984). Nelson (1993) suggested that demes might be defined in terms of the distribution of dispersal distances for juvenile male deer since they are responsible for the migration of genetic information. However defined, deer populations are highly genetically structured.

Ryman et al. (1981) used simulation modeling of deer and moose populations to show that certain hunting regimes could produce a severe loss of genetic variability in a short time period by altering demography. Their model made the unrealistic assumptions (for Upper Peninsula deer) that hunting mortality was random with respect to age and sex classes and that the sex ratio of the population was 40% males. They speculated that division of the population into sub-populations would further reduce genetic variability and that migration (dispersal) determined the relative levels of inbreeding in ungulate herds. More over, the switch from a natural to an essentially human-caused predatory regime may drastically alter the rates and patterns of genetic migration. Ryman et al. (1981) cautioned that their model predictions were conservative, especially noting that their sex ratio estimate may be severely biased toward males. Male-dominated or male-only hunting strategies will drive the effective population size down dramatically, increasing the risk of genetic drift and inbreeding depression.

Different inbred sub-populations will probably have different gene frequencies at many loci. Dispersal between demes should produce highly heterozygous individuals and a release from inbreeding depression (Cothran et al. 1983). Body size, nutritional condition. and size and symmetry of antler characteristics are positively correlated with heterozygosity. Deer with higher levels of genetic variability have greater antler size/Kg than those with low levels of variability. These effects are most pronounced in the first year of growth (Scribner and Smith 1990). Heterozygosity is also positively correlated with fetal growth rates, twinning rates, and maternal weights; all of which result in increased production (Cothran et al. 1983).

Deer social structure and mortality patterns in Michigan's Upper Peninsula suggest a situation conducive to the loss of genetic variation in spite of relatively high deer densities. Deer movements and the spatial geometry of the deeryards in the landscape suggest that deer sub-populations may be tied to traditionally-used seasonal ranges (Chapter 1). These sub-populations may or may not be synonymous with genetic demes depending on the degree to which they are genetically isolated.

In this chapter I describe the mortality patterns and age structure of northern Michigan deer that reflect a hunting regime that is strongly male-biased. Comparisons between 2 simulation models describe the population genetics of northern deer under the estimated mortality pattern and a hypothetical mortality pattern in which hunting mortality is not male-biased.

Methods

In conjunction with the concurrent study of deer movements (Chapter 1), deer were trapped in or adjacent to the Whitefish and Stonington deeryards in south-central Delta County, Michigan (Introduction). Stephenson-type box traps (Rongstad and McCabe 1984) were used at active winter timber cuttings where deer were attracted to the browse provided by slash and tops. Clover traps (Clover 1954, 1956) were used in more remote areas. All traps were baited with shelled corn. Trapping began in mid-January and continued until spring break up in late March or early April.

Deer were manually restrained and given color-coded, serially-numbered ear-tags. Deer were sexed and classified as fawn, yearling, or adult on the basis of tooth wear and replacement (Severinghaus 1949, Larson and Taber 1980). Canine teeth were extracted from a sub-sample of adults and aged via cementum annuli analysis (Gilbert 1966, DeYoung 1989a) to provide information on age structure.

A sub-sample of the trapped deer were fitted with radio-collars (Telonics Inc., Mesa AZ; Lotek Engineering Inc., Newmarket ON). Radio-collars were distributed among the various sex and age classes roughly in proportion to age/sex composition of the trapped sample. All radio-collars were equipped with a 12-hour, time-delayed, mortality switch.

I attempted to locate each radio-collared deer once each week from the time it was released until it either died, was determined to be censored, or the study ended (January 1995). Occasionally, signals from radio-collared deer become "lost" such that the fates of the animals are unknown. Such "lost" deer are termed "censored" to distinguish them from radio-collared deer whose fates (mortality or survival) are known. At least 3 extensive aerial searches were made for each "missing" deer before it was determined to be censored.

When mortality signals indicated that a deer had died, I located the carcass and performed a field necropsy to determine the cause of death. Predator kills were identified according to O'Gara (1978). Starvation was identified by the condition of the femur marrow (Thorne 1982).

Cause-specific mortality rates were estimated using MICROMORT software (Heisey and Fuller 1985). MICROMORT uses the Mayfield (1961, 1975) estimator which requires the researcher to designate intervals wherein the mortality rate is assumed to be constant (Heisey and Fuller 1985). For the purpose of analysis, I assumed that the biological year for deer began on 1 June with the birth of the fawn cohort. The year was then divided into 3 intervals coinciding with important life history events (Nixon et al. 1991a). The first interval (Summer, 1 June - 30 September) coincides with the birth of the fawns and spatial segregation of the sexes on the summer range. Interval 2 (Fall, 1 October - 1 January) coincides with Michigan's deer hunting seasons, the rut and the fall migration (Chapter 1). Interval 3 (2 January - 31 May) coincides with the winter yarding period and the spring migration (Chapter 1). All mortalities were classified as 1.) predation, 2.) starvation, 3.) hunting, and 4.) unknown. Predation mortalities that showed signs of severe malnutrition were classified as starvation since malnutrition was likely to be the ultimate cause of death. A fifth category was designated for censored individuals. Heisey and Fuller (1985) recommended bracketing true mortality rates in the presence of censored individuals by first assuming that all censored individuals had died and then assuming that all censored individuals had lived. Vangilder and Sheriff (1990) reported less bias and error in MICROMORT survival estimation when the radio-days accumulated by censored individuals prior to disappearance are included in the analysis. I followed Vangilder and Sheriff's (1990) recommendations for dealing with censored deer.

Age- , sex-, and interval-specific differences in mortality rates were examined using 2-tailed Z tests (Heisey and Fuller 1985, Nelson and Mech 1986, Nixon et al. 1991a).

I modeled the effects of the estimated mortality pattern on population genetics using Generalized Population Projection System (GAPPS, MT Coop. Wildl. Res. Unit) software. GAPPS is a discrete-time stochastic computer program that models animal populations by following individuals from birth to death. The model retains information on each individual's age, sex, parents, mates, offspring, membership in a family group, and if female, whether attended by offspring, pregnant, or solitary. Five events affect each individual during the simulation year: breeding, hunting mortality, natural mortality, births, and emigration. In addition, each modeled individual carries 2 alleles at a hypothetical locus. Newborns receive 1 allele from each parent in simple Mendelian fashion. GAPPS reports the total number of alleles in a population and population-wide heterozygosity. GAPPS also does pedigree analysis on newborns to determine the inbreeding coefficient, F (Harris et al. 1986, Harris and Allendorf 1989).

Two parallel models were constructed. Model A used the mortality rates estimated from the telemetry data which is characteristic of male-biased hunting. Model B was constructed with hunting mortality that was un-biased with respect to sex. Both used age-specific reproductive rates from Harder (1980), sex ratios at birth from Verme (1969), and age/sex specific dispersal probabilities from Nelson (1993). Reproduction and immigration were linear functions of population size subject only to the stochastic variation in the models. All dispersers entering the population were heterozygotes. Iterative adjustments of the reproductive and mortality schedules were made until both models ran at $r = 0$, where r is the intrinsic rate of increase (Caughley 1977). The mortality rate schedules of each model were made density-dependent according to a user-defined carrying capacity, K. As the model populations approached K, the mortality rates were at their maximum. As the populations grew less than K the mortality rates approached 0.

K values in the models were chosen to represent deme sizes. I could find no reports of deme sizes in terms of numbers of animals for deer or other large mammals. Nelson (1993), based on dispersal distances, reported that the spatial dimensions of demes in Minnesota deer were equivalent to circles with radii of 27 km. At summer densities of 0.25 to 5 deer/km^2 (M. Nelson pers. commun.), demes could contain as many as 10,000 deer which seems to be an upper boundary. Demes are defined as randomly-mating populations wherein all breeding males and females have equal probabilities of mating (Shields 1987). If fawns in Minnesota comprise 29% of the population and the adult sex ratio is 2 : 1 in favor of females (Nelson and Mech 1981), a deme size of 10,000 means that each male has an equal probability of mating with 4686 different females each breeding season. I ran the models at K values of 50, 100, 500, 1000, and 5000 to cover a range of possible deme sizes. Software restrictions prevented me from modeling deme sizes of 10,000. Simulations were 50 runs of 30 years. For each simulation, mean inbreeding coefficients (F), proportions of heterozygotes, number harvested, sex ratios and residual population sizes were compared between the 2 models using t-tests (Wilkinson et al. 1992).

Results

During the winters of 1991/1992 - 1993/1994, 507 deer were trapped and ear-tagged on the study area (Table 1, Chapter 1). I radio-collared 95 deer (Table 2, Chapter 1) and located them 4,599 times between January 1992 and January 1995 for a total of 38,888 deer-days.

Forty-nine mortalities were identified. Nine were due to predation. Coyotes (Canis latrans) killed an adult doe, a fawn doe, and a fawn buck. Black bears (Ursus americana) killed a fawn doe and 2 yearling bucks. One adult doe was killed by wolves (Canis lupus) and the predator(s) which killed the remaining 2 deer were not identified. One fawn doe and 5 fawn bucks died of malnutrition. Two adult does, 7 adult bucks, 1 yearling doe and 13 yearling bucks were shot legally. One adult doe was poached during the 1993 hunting season. For the purpose of mortality analysis, this poaching event was included with hunting mortality. Unknown or other mortalities took 5 yearling bucks, 1 fawn doe, and 5 adult does including 1 that was hit by a car. Eight adult does, 3 yearling does, and 1 yearling buck were censored. Five of the censored deer were wearing radio-collars that had been operating beyond the projected battery life, and 2 were known to have malfunctioning collars.

Table 7 gives the cause-specific mortality and the interval survival rates for the various sex and age classes of radio-collared deer. Annual survival was 0.88 for yearling does, 0.29 for yearling bucks, 0.77 for adult does, and 0.23 for adult bucks. Among yearlings, annual hunting mortality and annual unknown mortality rates were higher among bucks than among does (Table 8). Annual hunting mortality was also higher among adult bucks, although adult does had higher annual rates of mortality due to predation, and unknown sources. Adult does were also more likely to be censored (Table 8). During the winter, fawn bucks were somewhat more likely to starve ($P = 0.0910$) and fawn does were more likely to die from unknown causes ($P = 0.0272$). Predation rates for wintering fawns were equivalent for bucks and does ($P = 0.8966$).

Seasonal mortality (interval rates) was similar among the sexes for all age classes during the Winter. Fall mortality was significantly higher for bucks in the yearling and adult classes. Adult does had higher summer mortality than adult bucks, but the trend was reversed for yearling bucks and does (Table 9.).

Comparisons between adults and yearlings for annual cause-specific mortality indicated that adult does had higher mortality rate due to predation ($P= 0.0192$) and unknown causes ($P= 0.0188$) than yearling does. Adult bucks had higher hunting losses than yearling bucks ($P = 0.0292$), though yearling bucks had higher losses to unknown causes ($P = 0.0118$).

Comparisons between the cause-specific mortality of fawns, yearlings, and adults

Table 7. Survival and cause-specific mortality rates in radio-collared deer in Michigan's Upper Peninsula (after Heisey and Fuller 1985).

	Survival Interval			Radio			Survival		Mortality				
Age Class	Season	Length	Sex	n*	Radio days	Deaths	Rate	95% C. I.	Pred.	Starv.	Hunt.	Unknown	Cens.
Fawn (7-12 months)	Wtr/Spr	150	F	29	2716	7	0.68	0.51 - 0.90	0.09	0.05		0.18	
			M	31	3155	7	0.72	0.56 - 0.92	0.08	0.20			
Yearling	Summer	124	F	21	2503	1	1.00						0.04
(13 - 24 months)			M	24	2740	4	0.83	0.70 - 1.00		0.08		0.08	
	Fall	91	F	22	1785	1	0.95	0.80 - 1.00			0.05		
			M	13	1118	13	0.34	0.19 - 0.61			0.50	0.15	
	Wtr/Spr	150	F	20	2002	3	0.93	0.62 - 1.00			0.07		0.13
			M	20	757	0	1.00						
Adult	Summer	124	F	60	6824	10	0.90	0.82 - 0.97	0.02		0.02	0.07	0.06
(>24 months)			M	13	1612	0	1.00						
	Fall	91	F	68	4401	3	0.96	0.91 - 1.00			0.04		0.02
			M	4	809	12	0.29	0.14 - 0.60			0.71		0.06
	Wtr/Spr	150	F	50	6691	5	0.89	0.81 - 0.99	0.08			0.02	0.06
			M	13	662	1	0.80	0.51 - 1.00			0.20		

*The number of deer-records in the interval (data from 1992, 1993, and 1994 pooled)

Table 8. Sex class differences in annual cause-specific mortality rates for deer in Michigan's Upper Peninsula.

	Predation		Starvation		Hunting		Unknown/Other		Censored	
Age/sex Class	Rate	var(Rate)	Rate	var(Rate)	Rate	var(Rate)	Rate	var(Rate)	Rate	var(Rate)
Yearling Doe	0		0		0.108	0.00532	0		0.170	0.00810
Yearling Buck	0		0.083	0.00314	0.420	0.00980	0.209	0.00687	0	
Z statistic			-1.48		-2.54		-2.52		1.89	
P-value			0.1388		0.0110		0.0118		0.0588	
Adult Doe	0.081	0.00120	0		0.050	0.00079	0.083	0.00125	0.131	0.00187
Adult Buck	0		0		0.733	0.01080	0		0.062	0.00359
Z statistic	2.34				-6.34		2.34		0.93	
P-value	0.0192				0.0002		0.0192		0.3524	

Table 9. Sex class differences in seasonal mortality rates of deer from Michigan's Upper Peninsula.

	Summer		Fall		Winter/Spring	
Age/sex class	Rate	var(Rate)	Rate	var(Rate)	Rate	var(Rate)
Fawn Doe					0.321	0.00987
Fawn Buck					0.283	0.00814
Z statistic					0.28	
P-value					0.7794	
Yearling Doe	0		0.050	0.00235	0.072	0.00983
Yearling Buck	0.166	0.00571	0.655	0.01040	0	
Z statistic	-2.17		-5.36		1.04	
P-value	0.0300		<0.0002		0.2984	
Adult Doe	0.103	0.00159	0.041	0.00079	0.106	0.00201
Adult Buck	0		0.712	0.01680	0.203	0.00327
Z statistic	2.58		-5.06		-1.33	
P-value	0.0098		<0.0002		0.1836	

does during the winter revealed higher losses to unknown causes in doe fawns than in yearling (P = 0.0272). Adult does had higher predation rates than yearling does (P = 0.0376). Among bucks the only differences were higher rates of starvation among fawns relative to adults (P = 0.0120) and yearlings (P= 0.0120).

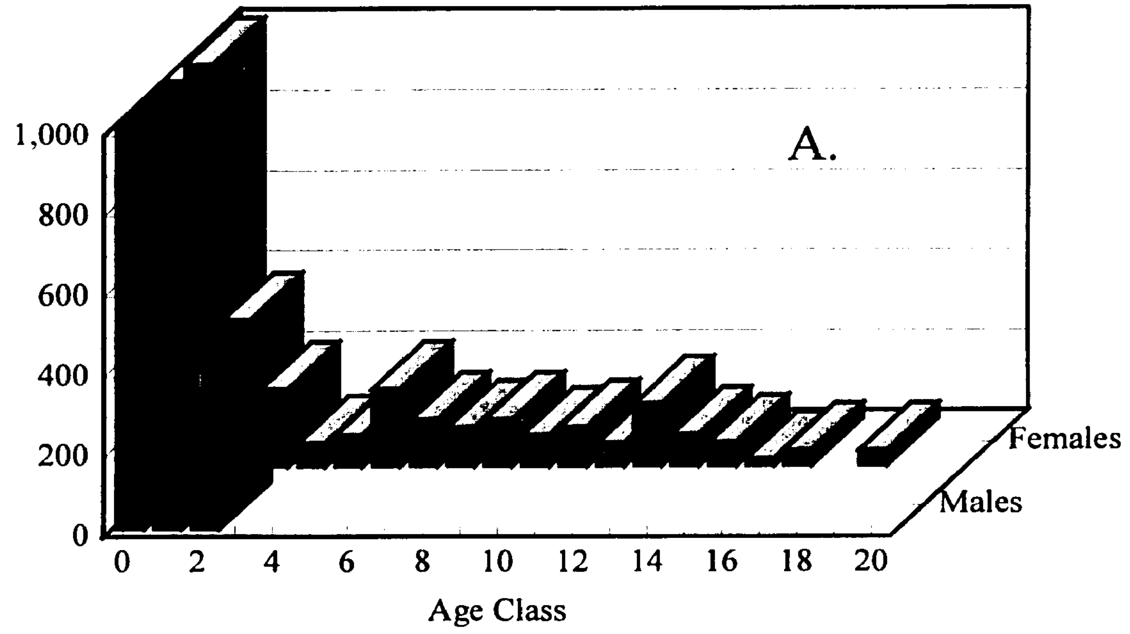
Age-related differences in seasonal mortality are given in Table 10. Among does, summer mortality was higher for adults relative to yearlings and winter/spring mortality was higher for fawns relative to adults and yearlings. Among bucks, both fawns and adults had higher winter/spring mortality than did yearlings.

I pooled the data from yearling and adult does to get a sample size large enough to compare seasonal mortality among migratory and non-migratory deer. Deer were considered migratory if their summer and winter ranges did not overlap (Chapter 1). Twenty-one migratory does and 20 non-migratory does yielded 10617 and 11095 deer days respectively. I detected no significant differences (P > 0.10) between the groups for seasonal mortality rates or annual cause-specific mortality rates.

Age and sex ratios were estimated from two sources. The first is simply the age and sex structure of the sub-sample of trapped deer that was aged by cementum annuli analysis (Figure 18a). The second (Figure 18b) is a projection of the age- and sex-specific mortality rate on an initial cohort of 2000 fawns (1000 of each sex). I assumed an initial 50% mortality in fawns (Dusek 1989). The latter method requires an assumption of constant mortality through time. Adult (>24 months) sex ratios were 26 : 1 in favor of females in the trapped sub-sample. Adult sex ratios based on mortality were 6 : 1 in favor of females.

Table 10. Age class differences in seasonal mortality rates for deer in Michigan's Upper Peninsula.

	Summer		Fall		Winter/Spring	
Age/sex class	Rate	var(Rate)	Rate	var(Rate)	Rate	var(Rate)
Fawn Doe					0.321	0.00987
Yearling Doe					0.072	0.00483
Z statistic					2.04	
P-value					0.0410	
Yearling Doe	0		0.050	0.00235	0.072	0.00483
Adult Doe	0.103	0.00159	0.041	0.00079	0.106	0.00208
Z statistic	-2.58		-0.16		-0.41	
P-value	0.0098		0.8728		0.6818	
Fawn Doe					0.321	0.00987
Adult Doe					0.106	0.00201
Z statistic					1.97	
P-value					0.0488	
Fawn Buck					0.283	0.00814
Yearling Buck					0	
Z statistic					3.14	
P-value					0.0016	
Yearling Buck	0.166	0.00571	0.655	0.01040	0	
Adult Buck	0		0.712	0.01680	0.203	0.00327
Z statistic	2.20		-0.35		-3.55	
P-value	0.0278		0.7264		0.0004	
Fawn Buck					0.283	0.00814
Adult Buck					0.203	0.00327
Z statistic					0.75	
P-value					0.4532	



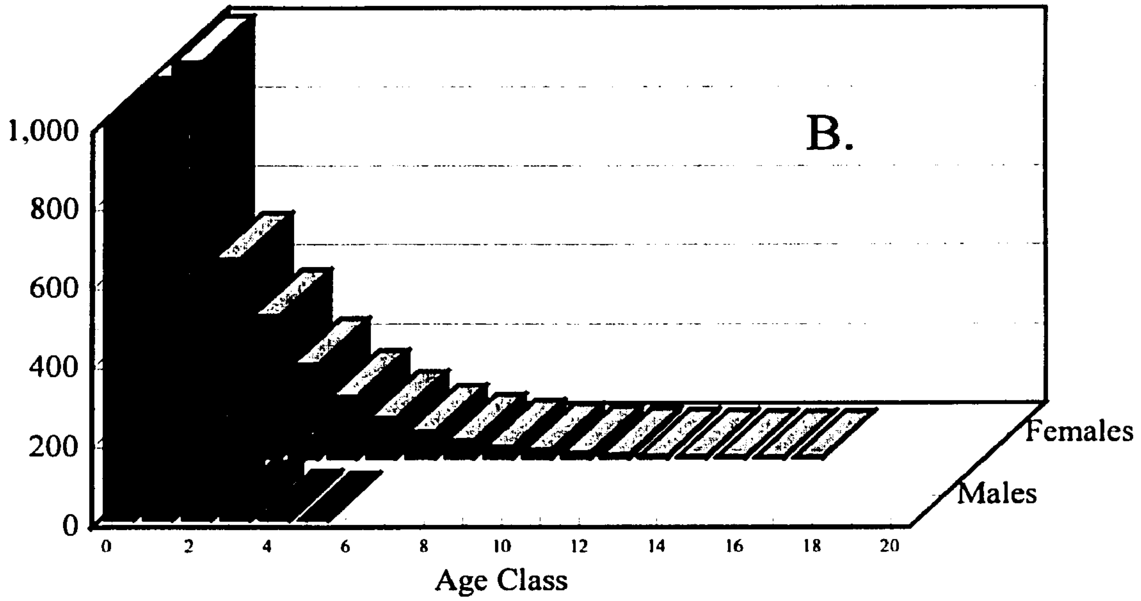


Figure 18. Sex and age structure of Upper Peninsula deer based on a trapped sample (A.) and calculated from mortality rates (B.). Figures are scaled to fawn cohorts (age class = 0) that are equal to 1000.

Comparisons of the simulation models revealed that mean F values and proportions of heterozygotes differed at each K (Table 11.). At K = 100, 500, and 1000, F was higher in Model A (male-biased hunting mortality). At K = 50, F was higher in model B (unbiased hunting mortality). The general trend in F for both models was a decrease in F as K increased (Figure 19). F could not be calculated at K = 5000 because of computer memory limitations. The proportion of heterozygotes was higher in Model B than in Model A for all K values. The proportion of heterozygotes in each model tended to decrease as K increased (Figure 20). Stochastic variation in both parameters was highest at small K values.

Table 11. Comparisons of simulated deer populations subjected to hunting that was male-biased (Model A.) and unbiased (Model B.).

		Model A		Model B			
K	Parameter^a	Mean	S.D.	Mean	S.D.	t	P-value
50	F	0.024	0.007	0.035	0.009	7.12	0.000
	Hetero	0.56	0.047	0.67	0.032	-47.4	0.000
	Ratio	18.9	16.0	0.90	0.10	7.98	0.000
	Pop	51.5	11.7	59.3	16.4	-2.76	0.007
	Imm	3.15	0.73	4.80	1.57	-6.72	0.000
	Yield	9.92	2.22	4.84	1.72	12.8	0.000
100	F	0.019	0.005	0.017	0.003	2.43	0.017
	Hetero	0.57	0.019	0.67	0.016	-27.5	0.000
	Ratio	17.7	2.10	0.89	0.093	56.6	0.000
	Pop	121.9	22.4	128.8	28.4	-1.35	0.182
	Imm	7.56	1.34	11.0	2.64	-8.26	0.000
	Yield	24.0	3.74	11.0	2.57	20.1	0.000
500	F	0.023	0.001	0.020	0.001	12.3	0.000
	Hetero	0.58	0.007	0.67	0.007	-67.9	0.000
	Ratio	17.1	1.10	0.89	0.033	104.2	0.000
	Pop	640.7	61.2	603.2	49.8	3.37	0.001
	Imm	40.4	3.65	51.6	4.62	-13.4	0.000
	Yield	125.0	11.0	54.3	4.8	41.6	0.000

Table 11. continued

		Model A		Model B			
K	Parameter	Mean	S.D.	Mean	S.D.	t	P-value
1000	F	0.023	0.001	0.018	0.001	24.9	0.000
	Hetero	0.57	0.006	0.66	0.006	-76.2	0.000
	Ratio	16.7	0.74	0.89	0.033	150.5	0.000
	Pop	947.7	53.9	903.7	36.5	4.772	0.000
	Imm	57.8	3.66	75.6	3.73	-24.1	0.000
	Yield	181.8	9.55	71.8	5.39	70.9	0.000
5000	F	**	**	**	**	**	**
	Hetero	0.56	0.003	0.64	0.004	-115	0.000
	Ratio	15.3	0.47	0.88	0.013	216.5	0.000
	Pop	3902.8	89.9	3831.3	27.3	5.38	0.000
	Imm	221.9	5.59	295.7	4.15	-75.0	0.000
	Yield	721.6	15.4	266.6	7.45	188.5	0.000

** Unable to calculate

ªParameters are Wrights F statistic (F), the proportion of heterozygotes (Hetero), the female : male sex ratio (Ratio), population size (Pop), the number of immigrants (Imm) and the number of deer harvested (Yield).

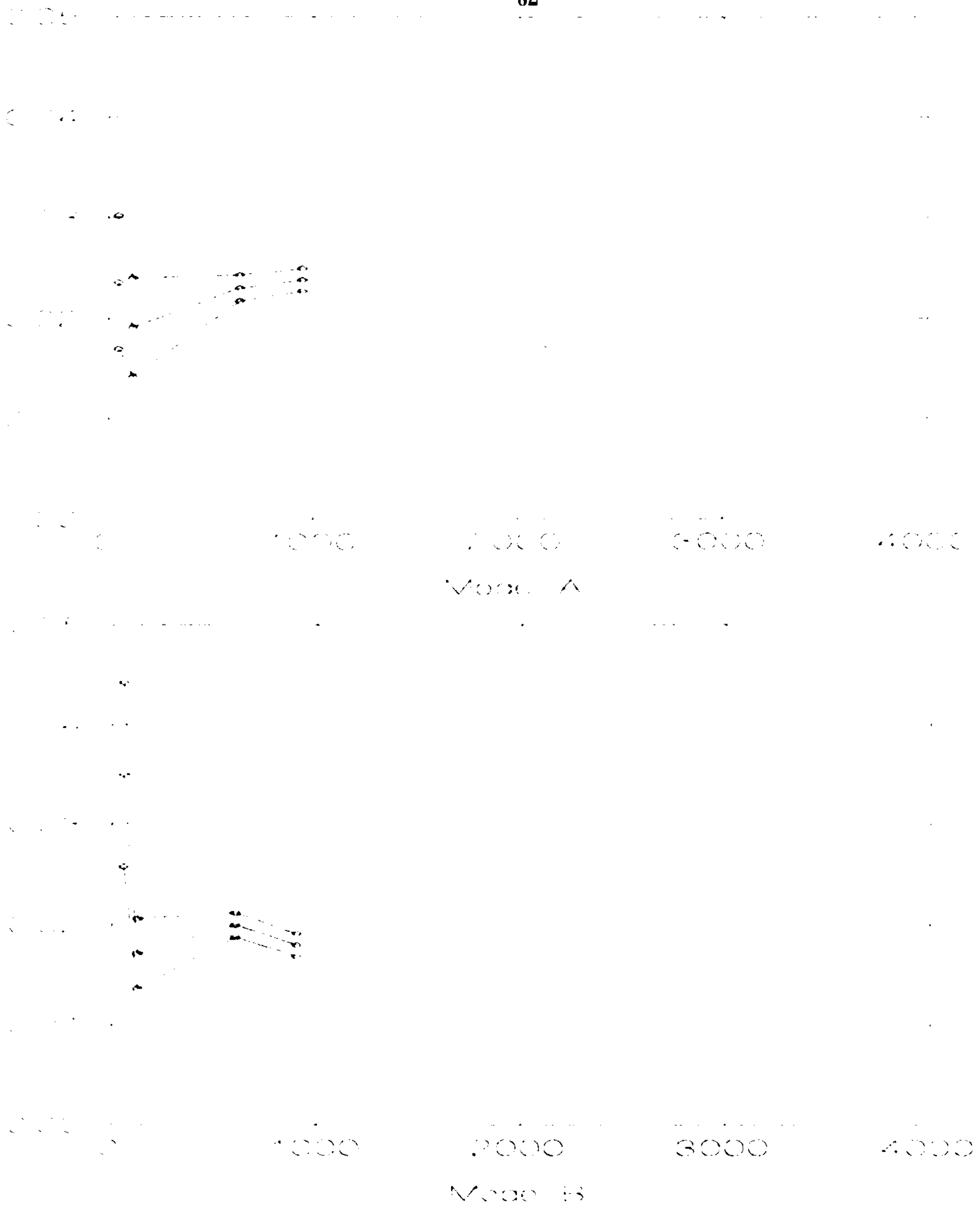


Figure 19. Trend in Wright's F statistic under male-biased hunting (Model A) and unbiased hunting (Model B). Center curve in each figure is mean F. Top and bottom curves are F + S.D., F - S.D.. X-axis is deme size. Software limitations prevented the the calculation of F when the models included more than 2000 individuals.

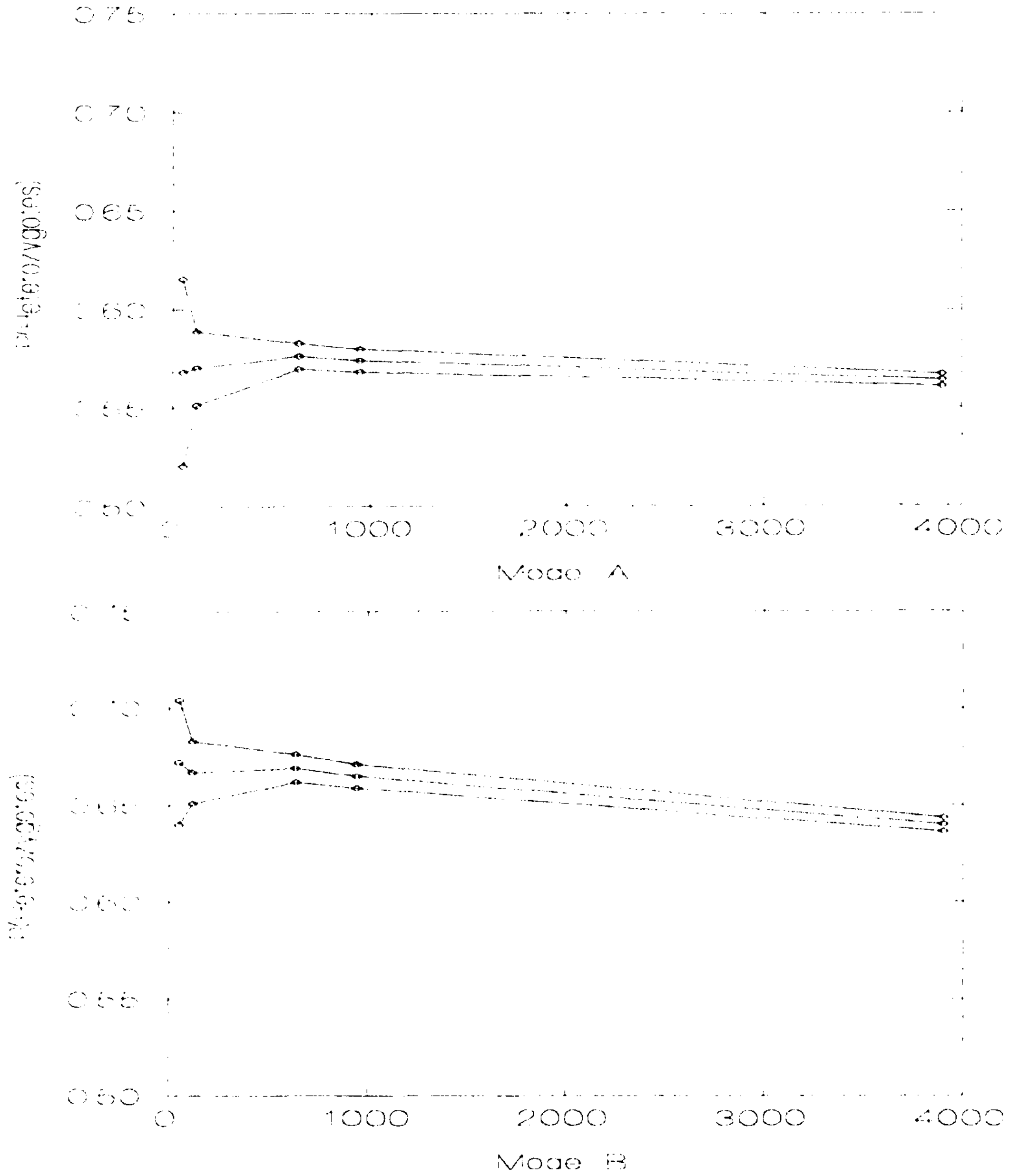


Figure 20. Trend in the proportion of heterozygotes under male-biased hunting (Model A) and un-biased hunting (Model B). Center curve in each figure is mean proportion of heterozygotes.. Top and bottomcurves are + and - 1 S.D.. X-axis is deme size.

Discussion

Nelson and Mech (1986b) recommended that approximately 600 deer days/death must be sampled to consistently obtain 95% confidence intervals < 0.10 on monthly survival estimates. This works out to about 20 deer/cohort/month. I had to pool data from all 3 years to get meaningful sample sizes for comparisons between cohorts and seasonal intervals. Fawn and yearling deer entered new cohorts on June 1 each year. Survival records for individual deer in the pooled sample are not strictly independent, for example an adult that was radio-collared in 1992 and tracked for 3 years would contribute 3 deer-years of survival data to the pooled data set. Given the sample sizes and duration of similar mortality studies, I believe that this treatment of the data is common. Short-term, intensive studies (3-5 years) such as this are cost effective but may fail to cover a wide enough range of environmental variation (Nelson and Mech 1986b).

PREDATION

The sources of mortality in this study are similar to those reported for other studies. Natural causes were mostly related to predation and starvation. Wolves (Hoskinson and Mech 1976, Nelson and Mech 1981, 1986a, 1986b, Kunkel and Mech 1994), coyotes (Huegel et al. 1985, Nelson and Woolf 1987, Nixon et al. 1991a), and bears (Kunkel and Mech 1994) are all known predators of mid-western deer. Bobcats (Felis rufus) and coyotes were the chief predators of deer in northern Michigan (Ozoga 1972). Feral dogs (Huegel et al. 1985) prey on deer as well but dog kills can be difficult to distinguish from coyote kills (Nelson and Woolf 1987). Bear predation is usually reported for neonates (Kunkel and Mech 1994, Ozoga and Verme 1982). Predation attributed to bears in this study could be animals that were killed by coyotes or bobcats and later scavenged by bears.

In this study predation was a minor source of mortality for all cohorts (Table 7). This contrasts sharply with Minnesota studies that reported high losses to wolf predation (Fuller 1990). For example, wolf predation may have limited recruitment in Minnesota (Nelson and Mech 1986b), killing more deer (especially adult bucks) during severe winters (Nelson and Mech 1986a). By way of contrast, wolf densities in northern Michigan are so low relative to deer densities that wolf predation is probably insignificant. Predation rates in northern Michigan are more similar to those in eastern Montana were predation was a minor source of mortality along the Yellowstone river (Dusek et al. 1989).

Predation rates for fawns would certainly be higher if I had measured fawn mortality during the summer. Nelson and Woolf (1987) attributed 11 of 16 known neonate mortalities to canid predators (coyotes and dogs) and fawn mortalities in Iowa were attributed to coyotes (54%) and dogs (23%) as well (Huegel et al 1985). Predation on Minnesota fawns was 49% bears and 51% wolves (Kunkel and Mech 1994).

STARVATION

Starvation during the winter can have profound effects on populations of northern deer, especially among fawns (Karns 1980). In spite of relatively mild winters (Chapter 1), I measured significant mortality among fawns (Table 7), most of which was probably caused by malnutrition. Jenkins and Bartlett (1959) reported that 80-90% of starvation mortality occurred among fawns. Over-winter survival may be more important than hunting season survival for Upper Peninsula deer (Ozoga 1969), although it is relatively minor for more southern populations (Nixon et al. 1991a). Moen (1978) reported a 2-year lag in the effects of high winter mortality that is felt when a diminished cohort of females enters the breeding population. Late springs in northern Michigan result in higher starvation mortality (Ozoga and Verme 1970), and estimated natal mortality of fawns varied between 10 and 50% depending upon the length of time that does are confined to the deeryards (Verme and Ozoga 1971). Winter starvation mortality is related to the fat cycle in northern deer. Winter length, severity and browse quality all interact to determine whether or not fat reserves last until spring green-up (Mautz 1978, Potvin and Hout 1983).

HUMAN-CAUSED MORTALITY

Human-caused mortality is common in northern deer. Hunting-related deaths are certainly the major source in exploited populations (Dusek et al. 1989). In Minnesota 45% of all mortality was due to hunting deaths during the firearm season, and hunting season mortality was 2-4 times higher for deer within 0.2km of a road. Changes in hunting regulations had the greatest impact on population change (Fuller 1990).

Hunting mortality in this study was highest in adult and yearling bucks (Table 7) reflecting a tradition of predominantly buck-only hunting regulations in Michigan that dates back to 1921 (Langenau 1994). Adults in this study had higher hunting mortality than yearlings in contrast to Minnesota where yearlings were most vulnerable (Nelson and Mech 1986b). Hunting mortality among yearling bucks in the Upper Peninsula is a function of weather and range conditions because a buck must have 3 inch (7.6 cm) or higher antlers to be harvested legally and antler development is associated closely with nutrition (Ryel et al. 1961). The higher hunting survival among yearling bucks in this study may reflect the fact that some of them did not yet have "legal" antlers.

Hunters are selective. Even when instructed to shoot the first deer that presented an unobstructed shot, hunters in southern Illinois shot larger (older) deer more frequently and yearling and 2 year-old bucks were most vulnerable (Roseberry and Klimstra 1974). "Any deer" regulations are not as efficient for harvesting does as "antlerless only" regulations because of hunter preference for large-antlered deer. Fall and annual mortalities in Illinois were lower for females than for males because harvest-related mortality dominated all known causes (Nixon et al. 1991a).

Male-biased hunting regimes result in an abnormally high percentage of small antlered young bucks (Matschke et al. 1984). Spike bucks were rare in central Illinois where hunters were free to shoot does and higher nutrition produces larger antlers (Nixon et al. 1991a). Hunting losses must balance an annual recruitment rate of 30-40% for the a population to remain stable. This is difficult to do when hunting is limited to bucks only (Matschke et al. 1984). Even under complete exploitation of adult bucks there was no loss in the productivity of a penned population because of breeding by yearlings (Ozoga and Verme 1985).

Other human-caused sources of mortality include poaching (Hoskinson and Mech 1976), car-kills and crippling losses. Crippling loss was 20-87% of the total reported legal kill in Illinois (Nixon et al. 1991a). Fall and winter mortality in the "unknown" category (Table 7) might be associated with crippling losses. Significantly higher unknown mortality among adult and yearling bucks would fit their status as legal quarry.

In eastern Montana, most (80%) mortality took place during the autumn hunting season, other sources included traffic deaths (11%), starvation (3%), and others (9%). Adult and yearling males were most vulnerable in spite of either-sex hunting. Fawns were selected against. Hunting and natural mortality were not compensatory (Dusek et al. 1989, 1992). In Illinois, annual survival of males varied between 41 and 87% with hunting and associated wounding as the principle causes of death (Nixon et al. 1994). Wounding loss was lower among older bucks, probably because hunters were willing to spend more time looking for them (Nixon et al. 1991a). Adult deer survival in Illinois was more dependant on the proximity to high-speed highways and to hunting than on habitat factors (Nixon et al. 1991b), and no deaths were due to winter or nutritional stress (Nixon et al 1991a). In Minnesota, wolf predation and human-caused mortality accounted for 95% of all known mortality and varied in importance between cohorts (Nelson and Mech 1986b), even though deer in the study area lived along the margins of wolf pack territories (Nelson and Mech 1981).

CENSORED DEER

Censored radios cause uncertainties in mortality estimates. Fuller (1990) assumed that signal loss after the expected life of the transmitter battery was due to battery failure. He also estimated that poaching losses were 31% of the legal harvest, which suggested an alternate explanation for censored collars. My treatment of censored individuals in estimating annual mortality was uniform among the sex and age cohorts although mortality probabilities differed with respect to sex, age, and time of year. Adult does are more likely to outlive their transmitter batteries after having been collared. Bucks are more likely to be shot and have their collars destroyed or go unreported, especially if they are censored during the fall. The presence of censored deer probably overestimates annual mortality among adult does and underestimates mortality among bucks and fawns.

ANNUAL SURVIVAL

In this study the annual survival of adult and yearling does was relatively high. Yearling and adult doe annual survival in other studies of northern deer was 55 - 61% (Nelson and Mech 1981),79 - 80% (Nelson and Mech 1986b), 78% (Dusek et al. 1989), and 69% (Fuller 1990). Yearling buck survival was low relative to Minnesota 59% (Nelson and Mech 1986b). Adult buck survival was also relatively low. Other estimates of adult buck survival include 37% (bucks-only hunting, Eberhardt 1960), 47% (bucks-only hunting, Nelson and Mech 1986b), 71% (trophy management, DeYoung 1989b), 40% (limited antlerless hunting, Dusek et al. 1989), and (46%, bucks-only hunting, Fuller 1990). In Minnesota, yearling survival was about the same as adults of the same sex (Nelson and Mech 1986b, Fuller 1990), but hunting and non-hunting mortality was higher for yearling Illinois bucks than for adults because of their socially-subordinate position (Nixon et al. 1994).

I was only able to estimate the winter portion of annual fawn survival (Table 7), but given the wide variation reported, annual fawn survival in the Upper Peninsula is probably not unusual. Fawn survival was estimated at 59 - 63% (Nelson and Mech 1981), 31% (Nelson and Mech 1986b), 50% (Dusek et al. 1989), 22% (Fuller 1990), and 89% (Nixon et al. 1991b).

Bartman et al. (1992) believed that high survival of adult females tempered a mule deer population's response to fluctuating weather conditions. The same may be true for white-tailed deer in the upper mid-west. Similar patterns were reported for Illinois where mortality was highest among yearling bucks and lowest among fawn bucks and adult does. Antlered buck and fawn survival were significantly lower than for yearling and older does. Fawn survival was high until weaning and remained high until family breakup in the spring. High fawn survival was attributed to high nutritional plane of prepartum does and postpartum fawns (Nixon et al. 1991a). In Minnesota, low fawn survival and reproductive rates were causing a declining population (Fuller 1990). By contrast, no sex- or age- specific differences in mortality from year to year were reported for a supplementally-fed captive herd in Pennsylvania (Woolf and Harder 1979).

Higher annual survival in does is no doubt due to differential hunting mortality, although higher doe survival was also reported for a non-hunted population (Gavin et al. 1984). Breeding season stress (Gavin et al. 1984) and use of less productive habitat by bucks (Beier and McCullough 1990) might be contributing factors.

SEASONAL MORTALITY

Seasonal mortality patterns differed between bucks and does (Table 9). Yearling and adult bucks experienced their highest mortality rates during the fall, again due to hunting. Yearling and adult does had the highest mortality during winter/spring. Yearling does and adult bucks had their lowest mortalities during the summer.

Summer mortality in most deer populations is relatively low except for neonates (Gavin et al. 1984, Dusek et al. 1989, Fuller 1990, Kunkel and Mech 1994). Ozoga et al.

(1982) found that neonate mortality is density-dependent among 1- and 2-year-old does due to the disruption of imprinting and social spacing at high densities. Fawns in Minnesota are a major prey source for wolves during the summer (Nelson and Mech 1986b). Low predator density and high nutrition apparently improve summer fawn mortality. No summer range killings were recorded in 60 deer-years of radio-tracking in Minnesota (Nelson and Mech 1981). Farmland deer in central Illinois had higher than 90% survival prior to the hunting season. Survival was highest during the summer because deer were dispersed across the landscape and human activities affecting deer survival were at a minimum (Nixon et al. 1991a).

Most fall mortality is associated with hunting, although northern deer may also be more vulnerable to predators during the fall migration since they are traveling through unfamiliar territory. In Minnesota, more deer were killed by wolves on the fall migration relative to the short amount of time spent migrating (Nelson and Mech 1991). The temporal distribution of buck mortalities in an unhunted insular population suggested that the ultimate cause of fall mortality was stress associated with breeding. Breeding season stress was due not to agonistic fighting among bucks but to the energy expended looking for does (Gavin et al. 1984).

Winter/spring mortality in northern deer is associated with the rigors of being confined to deeryards and the subsequent spring migration when the weather moderates. Winter mortality in this study was mostly classified as predation, starvation, and unknown (Table 7). Of the identifiable sources of mortality in yarded deer in another northern Michigan study, 53% were due to predation and 41% to starvation. Deeryard cuttings provide supplemental food, and where deer are supplementally fed, predation mortality is higher than starvation mortality (Ozoga 1972). Fuller (1990) reported that winter fawn survival was a function of increasing snow depth resulting in high losses to predation were predators were common and high losses to starvation where predators were uncommon. Bartman et al. (1992) reported that starvation and predation during the winter were density-dependent and compensatory for mule deer fawns. They believed that density dependent winter mortality rather than reproduction was responsible for population regulation.

Nelson and Mech (1986b) reported that most mortality occurred during the winter when grey wolf predation was an important source of mortality for all cohorts. Predation has been suggested as the primary force that shaped yarding behavior in northern deer because yarding facilitated lower predator:prey ratios, and trail systems develop which can facilitate escape (Messier and Barrette 1985). Nelson and Mech (1991) reported that winter mortality was higher in non-yarded does than in yarded does, although the same was not true for bucks.

SURVIVAL OF MIGRATORY AND NON-MIGRATORY DEER

The population I studied can be separated into migratory and non-migratory groups (Chapter 1). Differential hunting mortality among migratory and non-migratory deer created a discrete non-migratory population in Wisconsin (Dapson et al. 1979), and orphaned fawns loose the opportunity to learn migration traditions (Woodson et al. 1980). It is tempting to speculate that differential mortality may have fostered the development of a non-migratory faction in this study although no differences in the mortality patterns of migratory and non-migratory does could be detected. Gavin et al. (1984) believed that deer abandoned migratory behavior as habitat became more stable. Recent mild winters might have provided a measure of such stability.

SEX AND AGE STRUCTURE

However estimated, the age and sex structure of deer in this study reflected an adult population that is heavily weighted towards old does (Figure 18). Caughley (1974, 1977) stated that age ratios by themselves do not give information on age-specific population survival, fecundity, or growth rates without making the fairly restrictive assumption of a stable age distribution. Without this assumption, sex-specific age distributions serve mainly to illustrate the effects of differential mortality rates. Biases are inherent since trapped and harvested samples are not necessarily representative of the population (Fuller 1990). For instance, summer-trapped samples are male-biased relative to winter-trapped samples (Mattfeld et al. 1974).

Skewed sex ratios are the inevitable result of heavy buck hunting (Haynes 1984, Matschke et al. 1984), and have been reported for many populations. McCullough (1984) stated that short of no season at all, bucks-only hunting was the surest way to minimize the harvest. Bucks-only hunting regimes universally result in high residual populations that are primarily female, low overall recruitment, and legal bucks comprising 10% or less of the population.

Sex ratios at birth are usually 1:1 (Gavin et al. 1984), although Woolf and Harder (1979) reported that primary sex ratios favored females. Verme (1983) reported that fawns from undernourished does were biased toward males. Hunter preference for antlered males in Illinois resulted in a shift from a 1:1 ratio at birth to a 4:1 (F:M) ratio at 2.5 years (Nixon et al. 1991a). Sex ratio in an un-hunted insular population was 3 : 1 in favor of does due to differential mortality associated with breeding season stress (Gavin et al. 1984). Nelson and Mech (1981) believed that a 2 : 1 sex ratio in favor of does was the result of bucks-only hunting and differential predation. The mean age of adults was 6 years. In an earlier study, sex ratios were skewed by wolf predation which took mostly female fawns and adult bucks. (Hoskinson and Mech 1976). Sex ratios in Montana were 2:1 during the fall and 4:1 during the winter due to male-biased hunting under regulations that permitted limited antlerless hunting (Dusek et al. 1989). Higher mortality in Illinois bucks skewed the sex ratio towards does such that 70-80% of deer older than 4 years were female (Nixon et al. 1994). Car-killed deer from northern Michigan were mostly old does with very few old bucks (Ozoga 1972).

The sub-sample of trapped deer that were aged by cementum annuli analysis contained some remarkably old does (Figure 18a) including 1 13-year-old, 3 14-year-olds, 1 15-year-old, 2 16-year-olds, and 1 18-year-old. By coincidence the 18-year-old doe was also radio-collared. She died of unknown causes in April 1994 at the age of 19 years, 10 months - a longevity record in wild deer. Jenkins and Bartlett (1959) reported that few wild deer live past 10.5 years, and the oldest deer they aged was 17 years. Only 2-3% of bucks live to reach 5.5 years. Ozoga (1969) reported on the minimum ages for ear-tagged Michigan deer based on tag recovery. The oldest doe was 14 years 9 months, and the oldest buck was 8 years 5 months. Hoskinson and Mech (1976) aged 2 does at 12.9 and 13.8 years and reported that deer of these ages were rare in any population. In hunter-killed samples, only 1% of 17066 deer were older than 6.5 years (Erikson et al. 1961 in Hoskinson and Mech 1976) and 0% of 433 deer were older than 9.5 (Mech and Frenzel 1971 in Hoskinson and Mech 1976). The oldest deer reported for a non-hunted population were a 7.6-year-old buck and a 13.3-year-old doe (Gavin et al. 1984). The oldest deer reported in a Montana study were a 7-year-old buck and a doe aged at 13-15 years. Bucks older than 4 years were thought to comprise less than 1% of the male population. Females 3-7 years made up 32% and does older than 8 were 5% (Dusek et al. 1989).

Matson's Laboratory has aged over 10,000 white-tailed deer via cementum annuli analysis. Among 44 known-age deer, 38 were aged correctly, 3 were correct within 1 year, and 3 had were assigned ages that were >1 year off (Matson 1993). The histological condition of the teeth that I submitted was excellent. Cementum layers were unusually distinct which seems to be characteristic of samples from northern Michigan and northern Minnesota (G. Matson pers. commun.).

THE SIMULATION MODEL

Performance of the simulation models suggested that male-biased hunting regimes can effect the population genetics of deer across a broad range of deme sizes. The proportion of heterozygotes was significantly higher under unbiased hunting for all K values (Table 11, Figure 20). Inbreeding was significantly higher under male-biased hunting at K = 100, 500, and 1000. At K = 50 inbreeding was higher in the unbiased-hunting model, probably an artifact of the higher stochastic variability at low population levels. High levels of inbreeding are not expected with white-tailed deer because they are large, mobile animals with no apparent barriers to dispersal (Cothran et al.1983). Still, Nixon et al. (1994) found significant differences in F between sub-populations even though long distance dispersals would seem to assure plenty of genetic exchange. Genetic structure and the interaction of populations via dispersal creates levels of individual heterozygosities which have important theoretical and applied implications (Cothran et al. 1983). Nelson (1993) estimated 1,500 - 3,500 yearling (potential dispersers) / sub-population. Although dispersers are mostly male, male and female yearlings were equally likely to contribute their genes to neighboring sub-populations due to differential mortality and dispersal distance. He reasoned that domination by older bucks could reduce the potential gene flow mediated by dispersing yearlings. This may be especially true when yearlings suffer high hunting mortality. On the other hand, complete harvest of adult bucks may reduce a herd's genetic fitness due to a lack of a firm dominance hierarchy (Ozoga and Verme 1985).

Evidence for genetic structure in deer comes from morphological differences between adjacent sub-populations that were traced to habitat and genetic differences. At least 5 distinct genetic sub-populations were identified on the 78,000 ha Savanna River Plant (Smith et al. 1984), although specific descriptions of deme sizes in terms of numbers of deer are lacking. Smith et al. (1984) believed that it was critical to develop and define, in both a spatial and a temporal sense, the genetic characteristics of deer populations; and that management units should be based on these "natural populations".

Medin and Anderson (1979) simulated mule deer populations of 1.7 to 10.5 thousand individuals and advocated the use of simulation models for management decision-making. Fuller (1990) advocated the use of accounting models. One of the draw-backs of accounting models is that rates for age and sex classes are not synchronized so that changes in one parameter are not automatically compensated for by changes in another (McCullough 1984). This is why the simulation models in this study do not conform to McCullough's (1984) harvest model.

One of the problems of simulation modeling is that one can make small differences statistically significant by increasing the sample sizes of runs or simulations. Its more important to find out if modeling differences actually reflect biological differences. McCullough (1984) observed that the George Reserve population has gone through at least 2 severe genetic bottlenecks with no apparent ill effects on productivity. Individual deer populations may be robust to the loss of genetic variation as long as region-wide variability is maintained.

Management Implications

The mortality patterns of deer in the central Upper Peninsula are overwhelmingly shaped by male-biased hunting regulations. Survival estimates and age-structure comparisons between bucks and does suggest that the adult sex ratio is severely biased towards females. Deer populations hunted under bucks-only regulations yield neither more bucks nor more deer overall, and residual populations consist of high densities of primarily older does (McCullough 1984). Regarding bucks-only hunting, McCullough (1984:230) has observed...

> "Surely few professions have been cursed by such an intuitively appealing practice - one that is immensely popular with the constituents involved and that works in the diametrically opposite manner from which

> it is intended. It is ironic that those opposing hunting are most incensed by trophy hunting - the hunter's quest for large and inedible antlers - a practice that assures that the fewest deer will die of gunshots."

Control over deer survival via manipulation of hunting season regulations is the deer manager's most important tool - especially in areas were deer densities are believed to be too high. Restricting the kill to bucks makes this tool much less precise because the population response to hunting is more robust to bucks-only hunting than to un-biased hunting (Caughley 1977, McCullough 1984). Efforts to reduce deer populations to relieve browsing depredations will require a significant increase in antlerless harvesting.

In northern deer, starvation mortality during the winter can confound harvest management plans because starvation is a function of winter weather and can be quite variable (Ozoga and Verme 1971). Annual starvation losses are natural, even during mild winters. Managers should resist the temptation to treat normal starvation losses as a crisis that requires immediate attention, such as supplemental feeding. Emergency deeryard cuttings, designed to provide browse in the form of tops and slash, are counter-productive because they provide limited food (one year only), they further reduce the amount of thermal cover, and deeryard stands regenerate to mature thermal cover very slowly - if at all. Perhaps more antlerless permits can be issued following winters with low Winter Severity Indices so that harvests can track changes in population trends due to overwinter survival.

Simulation modeling suggested that strongly male-biased hunting regimes can effect the population genetics of northern deer populations at a wide range of deme sizes.

Specific effects differ at different deme sizes. Others have reported detrimental effects of male-biased hunting on the demographic patterns (Ginsberg and Milner-Gulland 1994) and population genetics (Ryman et al. 1981) of large ungulates. Calls for incorporating population genetics concerns in deer management (Cothran et al. 1983, Smith et al. 1984) are timely, although applications to deer management will require 1) a method for defining and measuring deme size, 2) a demonstration that the simulation models reflect biological reality, and 3) a demonstration that the effects are detrimental to the deer population's fitness.

Chapter 3: An evaluation of the thermal cover sub-model of a habitat suitability index model for white-tailed deer in the upper great Lakes for the Whitefish and Stonington deeryards.

Habitat suitability indices (HSIs) are theoretical models of wildlife/habitat relationships (Morrison et al. 1992). HSIs are based on the premise that habitat suitability can be related to habitat variables with primarily linear relationships (Farmer et al.1982, Best and Stauffer 1986), and that these variables can be combined into a meaningful index using a variety of weighting and averaging procedures. HSIs are scaled from 0 to 1 (Morrison et al. 1992) and are intended to represent the suitability of a given area of habitat to a given wildlife species (Laymon and Barrett 1986). Values of 1.0 represent the maximum habitat quality in a defined area (Shamberger and Krohn 1982). The relationships of the various variables represent numerous untested hypotheses, any one of which can be invalid for a particular application (Farmer et al. 1982).

HSIs are popular with land managers because they present a simple and understandable formulation of the major environmental factors thought to influence the occurrence and abundance of a species. They are valuable because they provide repeatable assessment procedures and indices of particular environmental characteristics that can be compared between alternative management plans (Shamberger and Krohn

1982, Morrison et al. 1992). HSIs can be especially useful for monitoring a species' habitat, provided one first demonstrates the degree of reliability and validity of the model (Morrison et al. 1992, Roloff 1994). Roloff (1994) tested HSIs for 9 wildlife species native to Michigan and determined that HSIs are a valid and useful tool for the comparison of large sample sizes and for landscape habitat quantification. Ideally, HSI models should accurately predict habitat suitability using variables from existing vegetation type maps or those derived quickly from remote sensing. Models that rely on field sampling of habitat variables will have limited usefulness for large-scale project planning because of the cost of obtaining the information (Laymon and Barrett 1986).

HSIs have been constructed for a number of vertebrate species (Morrison et al. 1992). They (and similar models) make the assumption that the distribution and abundance of a species can be predicted from habitat components (Marcot et al. 1983), in the absence of other population restrictions such as hunting. Errors in sampling and measuring habitat components and errors in defining what components are essential to a species can confound attempts to model wildlife-habitat relationships (Best and Stauffer 1986, Laymon and Barrett 1986, Roloff 1994). In addition, HSIs often assume that density is positively correlated with habitat quality (Van Horne 1983, Best and Stauffer 1986). This latter assumption has been the basis for a wide range of management decisions and can be violated by a number of situations including time lags in the population response to habitat changes, confounding social and behavioral patterns, and inter-specific interactions (Farmer et al. 1982, Lancia et al. 1982, Van Horne 1983, Flather and Hoekstra 1985, Laymon and Barrett 1986). Common traits of species whose density does not correlate with habitat quality include social dominance patterns, high reproductive capacity, and habitat generalization (Van Horne 1983). Van Horne (1983) recommended that demographic patterns such as survival and production be incorporated into a definition of habitat quality; but until more efficient population assessment techniques are developed, animal abundance will continue to be used as an index of habitat quality (Roloff 1994).

Validation is the process of determining the usefulness and accuracy of model predictions and of model implementation in impact assessment, and management planning. Validation provides confidence intervals for use in management decisions, tests of the adequacy of existing habitat inventory data for predicting a species response, and for the identification of faulty assumptions and faulty construction (Marcot et al. 1983). Several authors have cautioned against using untested models for habitat management (Laymon and Barrett 1986, O'Neil et al. 1988, Block et al. 1994). Lancia et al. (1982) and Laymon and Barrett (1986) gave guidelines for testing HSI models.

Bender and Haufler (1990) developed a relatively elaborate white-tailed deer HSI (WTDHSI) for the upper Great Lakes region. The model evaluates habitat suitability for deer via four sub-models which correspond to four important habitat components: 1) Fall and Winter Food, 2) Spring Food, 3) Security Cover, and 4) Thermal Cover. Weber et al. (1983) described how predictive models of deer/habitat relationships might be incorporated into forest planning.

Roloff (1994) partially validated the WTDHSI by correlating the Fall-winter food and Security Cover sub-models with pellet-group counts (Eberhardt and Van Etten 1956, Ryel 1971, Mooty 1980), an index of deer density. The optimal scale of applicability for these portions of the model was estimated at 16.4 ha, and the sub-models were significantly (P=0.10) correlated with pellet-group counts.

This chapter describes a similar evaluation of the Thermal Cover sub-model of the WTDHSI using pellet group density as an index of the intensity of deer use. Lancia et al. (1982) reported that the best test of a habitat model is to examine how closely model predictions reflect habitat selection by the species being modelled. Living at the northern edge of their range, deer in the Upper Great Lakes seek out wintering areas where thick conifer canopies provide shelter (Thermal Cover) from wind and cold (Blouch 1984). The Thermal Cover sub-model of the WTDHSI assumes that 5 variables can adequately describe the quality of deer wintering areas (See Bender and Haufler [1990] for justification): 1) percent conifer canopy closure, 2) site index for northern white cedar, 3) size of the area, 4) Basal area, and 5) dominant overstory species. Figures 21 and 22 show the assumed relationships between habitat suitability and the five variables. The 5 variables are assumed to be equally important and their suitability scores are simply multiplied to arrive at the Thermal Cover sub-model suitability index (Bender and Haufler 1990).

Weber et al. (1983) described a discriminant function that could separate deeryard stands from similar non-deeryard stands in northern New Hampshire on the basis of site index for red spruce (Picea rubens), average elevation, stand size, total basal area, percent conifer canopy closure, range of elevations, and number of overstory species.

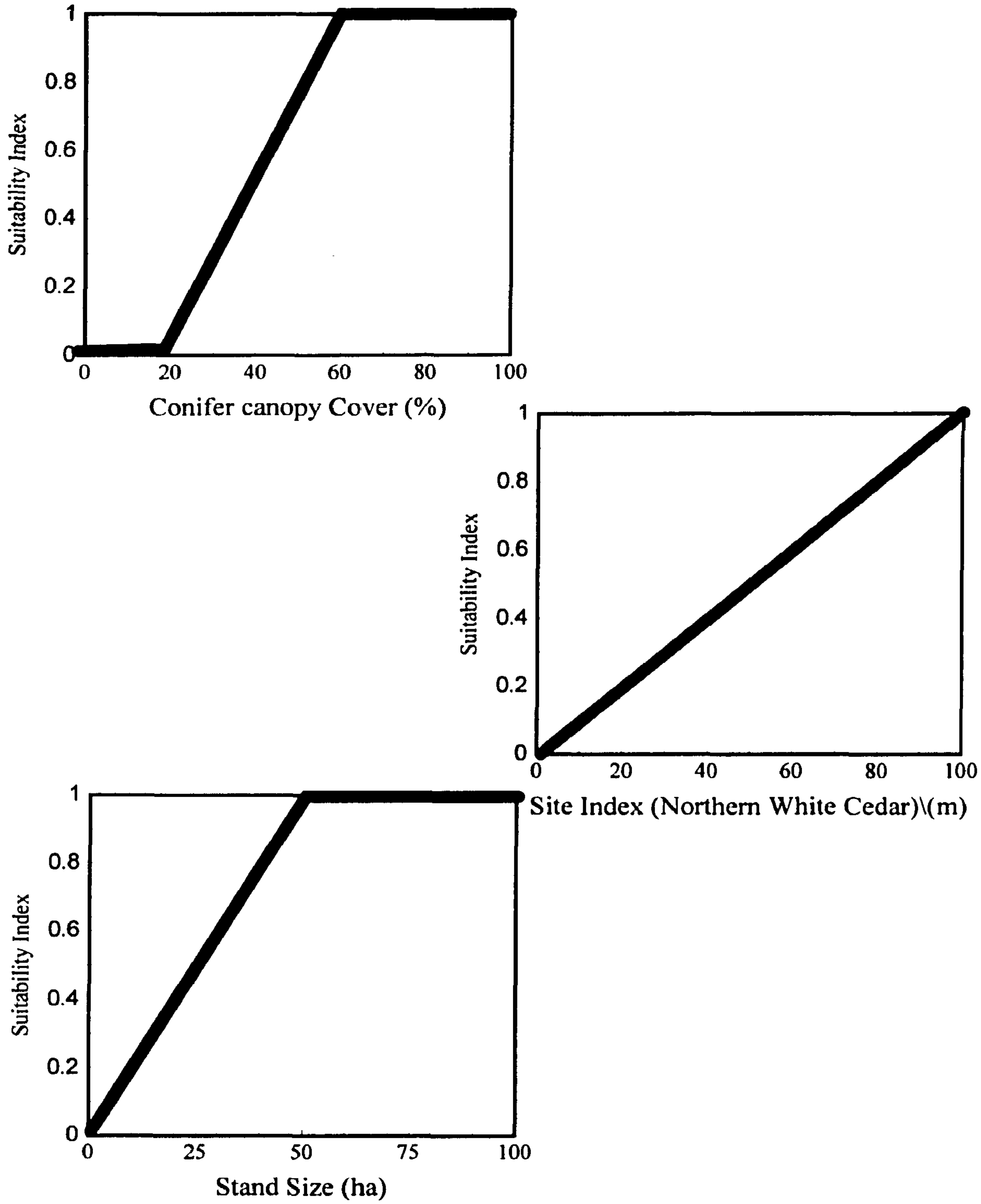


Figure 21. Assumed habitat suitability relationships between conifer canopy cover, site index for Northern White Cedar, and stand size (Bender and Haufler 1990).

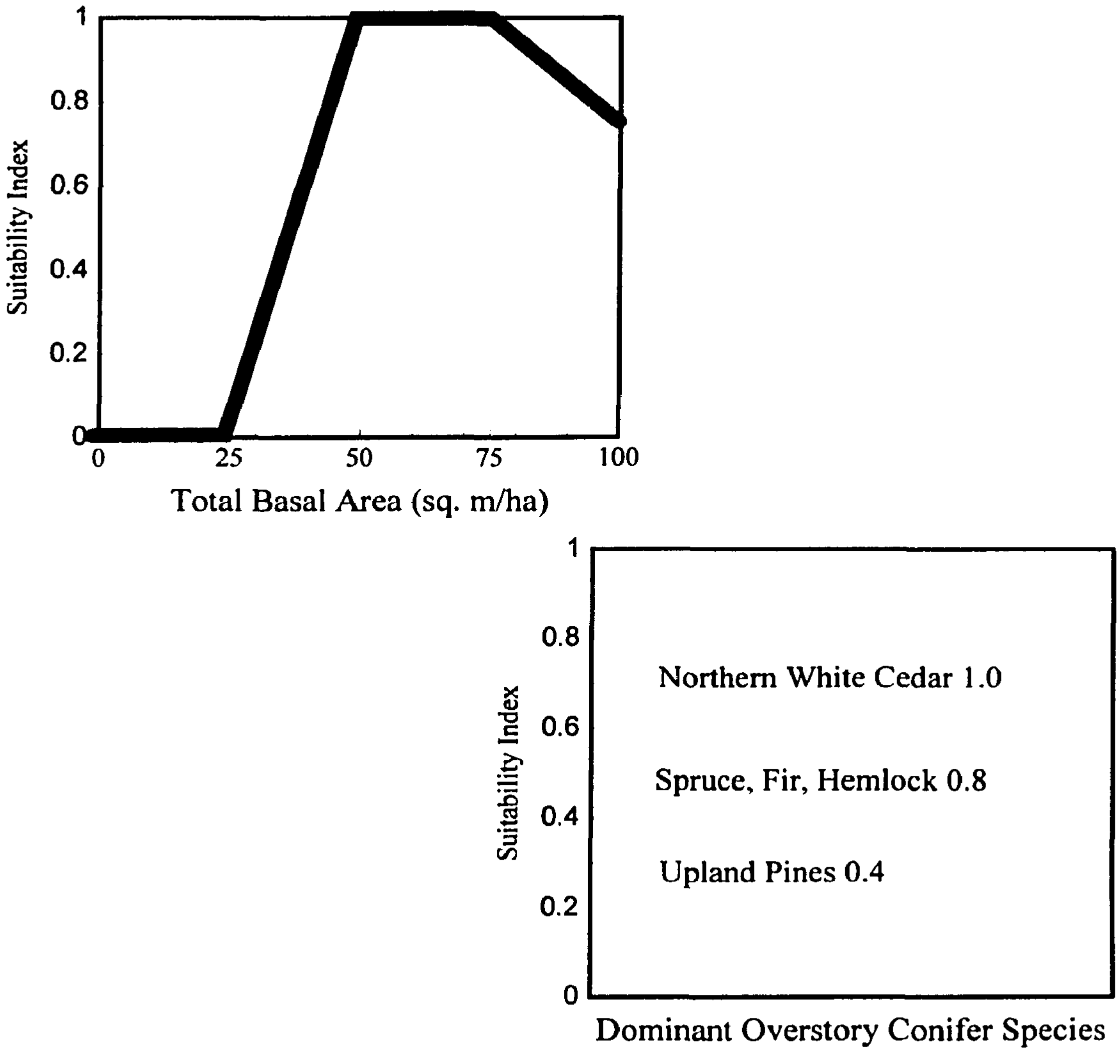


Figure 22. Assumed habitat suitability relationships between total basal area and dominant overstory conifer species (Bender and Haufler 1990).

Study Area

I sampled Thermal Cover variables in the Whitefish and Stonington Deeryards, located in southern Delta county, Michigan (see detailed description in the introduction). Study area boundaries were determined by "core deeryard" maps published by the Michigan Department of Natural Resources in 1977. Similar maps from 1967 and 1958 suggest that these areas have been used by wintering deer for more than 35 years.

Methods

Fifty randomly-located plots were established in each deeryard. Plots consisted of a central point with 1m x 25m transects extending in each of the 4 cardinal directions. Sub-model variable measurements and pellet-group counts were made at each plot. I estimated percent conifer canopy closure using a spherical densiometer (Forest Densiometers, Arlington VA), and averaging the values measured at the terminal ends of the 4 transects at each plot. Cedar site index was estimated from the height and age at DBH of a representative codominant cedar (Gevorkiantz 1956). If no cedar were present at a plot, a "missing value" was recorded for cedar site index. Stand size was estimated from 1993 digital cover type maps that were provided by the Michigan Department of Natural Resources using PC-ARCINFO (ESRI Corp., Redlands CA). Delineation of stand boundaries was based on a principle components transformation of Landsat Thematic Mapper imagery (Eosat Inc.). This process identified 13 non-coniferous and 17 coniferous cover types. Conifer cover types other than Pine (Pinus) and tamarack (Larix laricina) were further delineated to those that had >70% crown closure and those that had < 70% crown closure (Maclean Consultants Ltd. no date). Basal area was measured with a ten-factor prism at the center of each plot. Dominant overstory conifer species was estimated visually. Habitat variables were sampled during March and April 1993.

Deer density was indexed by pellet-group density. Using the random plots as a center point, pellet-groups (Eberhardt and Van Etten 1956) were counted along the 4 25m transects at each plot. Pellet-group counts were done during March and April 1992, 1993, and 1994 (Chapter 1).

Thermal Cover suitability scores were calculated using the 5 habitat variables following Bender and Haufler (1990). I use Pearson's Correlations (Wilkinson et al. 1992, Sokal and Rohlf 1995) to examine the relationship between pellet-group density and the variable measurements; and between pellet-group density and the Thermal Cover suitability scores for the 5 variables. Kruskal-Wallis and Mann-Whitney U tests (Lehman 1975, Wilkinson et al 1992) were used to test if dominant overstory conifer species or Thematic Mapper cover types affected pellet-group density. Tests were considered significant at P = 0.10.

Two measures of pellet-group density were used in the analysis. The first (PG93) was the pellet group density measured at each plot in 1993 (same year as the habitat sampling). The second (AVGPG) was the average of the pellet group densities measured in 1992, 1993, and 1994 at each plot.

Results

Mean PG93 was 7.34 pellet groups/100m^2 (SD = 8.96, range: 0 - 62, n = 100). Mean AVGPG was 18.58 pellet groups/100m^2 (SD = 14.4, range: 2 - 94, n = 100).

Plots fell in 12 Thematic Mapper cover types (Table 12). Cover type had no effect on PG93 (KW = 10.303, P = 0.503), or AVGPG (KW = 16.368, P = 0.128).

Mean percent conifer canopy closure was 37.5% (SD = 26.3, range: 0 - 94, n = 100), and was significantly correlated with PG93 (r = 0.207, P = 0.039, n = 100). It was not correlated with AVGPG (r = 0.019, P = 0.848, n = 100). Suitability scores for percent conifer canopy closure averaged 0.358 (SD = 0.366, range: 0 - 1.0, n = 100), and were not correlated with PG93 (r = -0.077, P = 0.447, n = 100) or AVGPG (r = 0.150, P = 0.136, n = 100).

Mean site index for cedar was 9.42m (SD = 2.80, range = 3 to 17, n = 69), and was not correlated with PG93 (r = -0.026, P = 0.833, n = 69). The correlation between site index for cedar and AVGPG was significant (r = 0.236, P = 0.051, n = 69). Suitability scores for site index for cedar averaged 0.877 (SD = 0.156, range: 0.3 - 1.0, n = 69), and were not correlated with PG93 (r = 0.069, P = 0.574, n = 69) or AVGPG (r = 0.191, P = 0.116, n = 69). Site index for cedar could not be measured at 31 plots.

Mean basal area was 24.6m^2/ha (SD = 15.7, range = 0 to 66.6, n = 100), and was not correlated with PG93 (r = 0.083, P = 0.414, n = 100) or AVGPG (r = 0.025, P = 0.806, n = 100). Suitability scores for basal area averaged 0.233 (SD = 0.336, range: 0.0 - 1.0, n = 100), and were not correlated with PG93 (r = -0.023, P = 0.812, n = 100) or AVGPG (r = 0.047, P = 0.640, n = 100).

Mean stand size was 171ha (SD = 346, range = 0.74 - 1923, n = 100), and was not correlated with PG93 (r = 0.019, P = 0.851, n = 100) although the relationship with

Table 12. Thematic Mapper cover type classification of sample plots.

Cover Types	Number of plots
Wet hardwood/conifer mix	33
Mixed conifer, >70% canopy closure	25
Northern Hardwoods	13
Ag./cropland	7
Dry hardwood/conifer mix	6
Herbaceous open land	3
Mixed conifer, <70% canopy closure	3
Mixed pine	3
Tamarack	3
Aspen/birch	2
Black spruce >70% canopy closure	1
water	1

AVGPG was significant (r = 0.195, P = 0.052, n = 100). Suitability scores for stand size averaged 0.633 (SD = 0.393, range: 0 - 1.0, n = 100) and were not correlated with PG93 (r = -0.077, P = 0.447, n = 100) or AVGPG (r = 0.150, P = 0.136, n = 100).

Under the dominant overstory conifer species variable, 37 plots were classified as northern white cedar (suitability score = 1.0), 38 as spruce-fir-hemlock (suitability score = 0.80), 0 as upland pine (suitability score = 0.4), and 25 as other (suitability score = 0.0). PG93 differed among the dominant overstory canopy species classifications (KW= 6.756, P = 0.034) with the "other" category having the lowest as well as the most extreme average rank. With the "other" category removed, there was no difference in pellet group densities between plots classified as northern white cedar and those classified as spruce-fir-hemlock (U = 605, P = 0.297). The difference in AVGPG among dominant overstory species classification was also significant (KW = 5.556, P = 0.062). With the "other" category removed, AVGPG was higher on northern white cedar sites than on spruce-fir-hemlock sites (U = 529.5, P = 0.066).

I calculated Thermal Cover sub-model scores using 2 treatments for missing values for site index for cedar. For the first, I assigned missing values the average value calculated for the 69 plots where site for index for cedar was measured. For the second, I eliminated plots that were missing values for site index for cedar.

Under the first method, mean sub-model scores were 0.068 (SD = 0.169, range: 0 - 1.0, n = 100) and were not correlated with PG93 (r = -0.051, P = 0.615, n = 100) or AVGPG (r = 0.084, P = 0.405, n = 100).

Under the second method, mean sub-model scores were 0.086 (SD = 0.190, range:

0 - 1.0, n = 69) and were not correlated with PG93 (r = -0.094, P = 0.443, n = 69). The relationship with AVGPG was significant (r = 0.200, P = 0.100, n = 69).

As an alternative method of calculating the sub-model Thermal Cover score, I averaged the suitability scores for the 5 variables rather than multiplying them as outlined in Bender and Haufler (1990). The two treatments of missing values for site index for cedar remained the same.

Under the first treatment of missing values for site index for cedar, the alternate sub-model scores averaged 0.558 (SD = 0.194, range: 0 - 1.0, n = 100) and were not correlated PG93 (r = 0.116, P = 0.250, n = 100) or AVGPG (r = 0.084, P = 0.405, n = 100).

Under the second treatment of missing values for site index for cedar, the alternate sub-model scores averaged 0.605 (SD = 0.190, range: 0.2 - 1.0, n = 69) and were not correlated with PG93 (r = 0.023, P = 0.854, n = 69). The relationship with AVGPG was significant (r = 0.200, P = 0.100, n = 69).

Discussion

As a test of the Thermal Cover sub-model of the WTDHSI, this analysis suffers from the basic problem that all of the sample plots were within an area identified as a deeryard. As designated, deeryards in the central Upper Peninsula are areas that are heavily used by wintering deer and contain a high proportion of stereotypical deeryard stands (dense swamp conifer) interspersed with other deciduous, upland, and non-forested cover types. Seventy-one percent of the sample plots were in cover types that had a conifer component in the overstory (Table 12), indicating that they represent potential deeryarding areas in terms of shelter. The remaining 29% of the plots were in areas with no overstory conifer component. Non-deeryard plots in the study area probably receive higher over-winter deer use relative to similar areas that are not in identified deeryards because of their proximity to stereotypical deeryard stands and high numbers of wintering deer. This bias probably explains the fact that cover type had no effect on PG93 or AVGPG.

This analysis is further confounded by the use of pellet-group counts as an index of deer use. Sample design, environmental conditions, site-specific differences, and observer biases affect pellet-group counts (Neff 1968). These combined effects of potential biases were so severe that Fuller (1991) reported that there appears to be no way to clearly interpret a single year's pellet-group data and that a series of annual counts needs to be interpreted with caution. I suspect both PG93 and AVGPG suffer from observer bias since different field personnel assisted with pellet-group counts within years and between years.

Deer possess all the traits commonly associated with species whose density does not correlate well with habitat quality (Van Horne 1983). Even so, the performance of the Thermal Cover sub-model of the WTDHSI was disappointing. Morrison et al. (1992) reported that HSIs can be expected to account for roughly half the variation in density of abundance of a species at best, less so for migratory species. The square of the r value in a correlation is an estimate of the amount of variation in one variable that can be explained by variation in a correlated variable (Sokal and Rohlf 1995). None of the r values in these tests approached the $r = 0.71$ that would give an r^2 of 0.50.

Based on its significant but weak correlation with PG93, percent conifer canopy closure may a useful variable for modeling thermal cover value. Mean suitability scores were somewhat low although the standard deviation and range of values indicated that a suitable range of different percent conifer canopy closure values was contained in the data set. Since the suitability scores were not correlated with PG93 or AVGPG, the assumed relationship between percent conifer canopy closure and thermal cover value should be re-evaluated.

Site index for cedar had a significant though weak correlation with AVGPG, suggesting its potential for modeling winter deer habitat. Lack of correlation between the suitability scores and the pellet-group densities suggests that the assumed relationship between site index for cedar and thermal cover value needs to be re-evaluated. High mean values and high mean suitability scores indicate that the range of possible suitability scores is prematurely truncated at 1.0.

Neither basal area nor its suitability scores were correlated with PG93 or AVGPG. In addition, basal area thermal cover suitability scores were consistently low. In northern New Hampshire deeryards, total basal area was inversely related to deer occupancy (Weber et al. 1983). Dropping the total basal area variable or changing it to conifer basal area may improve the model.

Stand size had a significant though weak correlation with AVGPG, suggesting that it may be useful for modeling winter deer habitat. Mean values and suitability scores were somewhat high, indicating that the suitability scores may have been prematurely truncated at 1.0. Lack of correlation between suitability scores and pellet-group density warrants re-evaluation of the assumed relationship between stand size and winter habitat value.

Dominant overstory species score showed a difference in PG93 and AVGPG between plots classified as "cedar", "spruce-fir-hemlock", and "other". This suggest that cover type may be useful in modeling winter deer habitat.

Poor correlation or lack of correlation between the habitat variables and pellet-group density may preclude building other models with these same variables. Such "Data-fitting" may be a poor strategy for validating HSI models because it requires that one be certain that density estimates are representative of limits imposed by the habitat. It may be better to critically examine the individual assumptions in the model (Farmer et al. 1982). O'Neil et al. (1986) cautioned that changes that improve model correlations should not be made unless they can be justified biologically.

The sub-model assumption that all 5 habitat variables are equally important in determining the quality of wintering habitat is probably not true. That percent conifer canopy closure, site index for cedar, and stand size were correlated with one of the pellet-group density measurements while basal area was not suggests that some variables have more influence on winter habitat quality than other variables. Elaborate HSI models often suffer from too much information. The sensitivity to one variable diminishes as more variables are added to the model such that HSIs may not accurately reflect actual habitat effectiveness or population responses (Morrison et al. 1992).

Sub-model scores were surprisingly low for an area traditionally-used by wintering deer. Simply multiplying the various suitability scores for the habitat variables means that the Thermal Cover score can only ever be as high as the lowest of the suitability scores. In this case, I suspect that the low suitability scores for basal area were depressing the sub-model scores artificially. The alternative method of combining individual suitability scores (averaging them instead of multiplying them) preserves the assumption that all the variables are equally important but gives higher sub-model score such as would be expected in a known deeryard. A better approach may be to determine the importance of the habitat variables in determining habitat quality relative to each other, and weighting them accordingly or eliminating the less important ones.

This analysis is also confounded by issues of temporal and spatial scale. The sampling period for PG93 or the habitat variables was not the three year minimum as suggested by Marcot et al. (1983). Plot size was probably too small. Spatial scale affects HSI performance and should reflect size of the species home range, degree of specialization, habitat heterogeneity, and intended use of the model (Laymon and Barrett 1986). My random plots were smaller that 1 ha. Deer winter ranges were estimated to be about 200 ha (Chapter 1). Roloff (1994) found that other sub-models in the WTDHSI worked best at a scale of measurement equal to 16.4 ha and recommended that generally HSIs should be evaluated at scales equivalent to that of the studied species' home range. Laymon and Barrett (1986) recommended that HSIs be evaluated at scales equal to 1/4 that of a species' home range.

Evaluation of the Thermal Cover sub-model at spatial scales approaching that of deer home ranges would require modification since all the sub-model variables are stand-level measurements. A 200 ha area in the Upper Great Lakes is likely to encompass parts of several different stands each having different values for the sub-model's variables. Roloff (1994) described how to link HSIs with habitat variables that are stratified by combinations of cover type and ecological land type classification. HSI scores can then be calculated at appropriate scales using area-weighting procedures.

Management Implications

Habitat modeling is an iterative process which requires that theoretical models be evaluated and re-evaluated with field data to arrive at validated models useful for monitoring a species' habitat. This study is an initial step in the validation process for the Thermal Cover sub-model of the WTDHSI. Comparisons of vegetation maps with maps of known deer yards indicate that not all conifer swamps in the Upper Peninsula are used equally as deeryards. Assessment of the distribution of deeryard swamp-conifer stands and non-deeryard swamp-conifer stands on a regional basis requires a habitat modeling approach.

Results of this analysis suggest that the Thermal Cover sub-model as written may be a poor descriptor of known deeryards. Averaging the individual suitability scores instead of multiplying them (Bender and Haufler 1990) seemed to improve its performance. Evaluation of the individual variables suggests that the basal area variable should be eliminated or changed. Methods of weighting the variables must be explored.

Further validation work should be done in areas both inside and outside of known deer yarding areas to legitimately test the sub-model's ability to identify potential wintering areas for deer, with more attention paid to the effects of the spatial scale of measurement. An alternate (and more precise) index of deer use needs to be identified.

Management Summary

The management of deer populations relative to browsing impacts in deeryards has been an intractable problem since the earliest attempts at formal deer management in the Upper Great Lakes. Stand-level solutions (short of fencing off impacted stands) are destined to failure because the key components of deer behavior that cause intense browsing in some areas (seasonal migration, tradition mediated by social structure) operate at a landscape scale. This is the case for individual family groups, but it is even more imperative for aggregates of family groups that are tied to specific deeryards in the landscape. Mortality patterns characteristic of bucks-only hunting regimes only exacerbate the problem because they encourage high densities of deer that are mostly off-limits to legal hunting.

In a landscape sense, we still do not know the full scope of the problem of balancing deer with other management goals in the northern forest. Comparisons of recent vegetation maps with maps of known deeryards suggest that there may be deeryard-type stands that are not used as deeryards and thus, not subject to browsing effects. These stands have not been quantified, compared with known deeryard stands, nor investigated to see whether or not they are truly (or relatively) free from the browsing pressure of wintering deer. For these reasons, it is difficult to say whether or not non-deeryard swamp conifer stands across the landscape can serve as reservoirs of plant diversity by providing refuges for plants that are sensitive to deer browsing.

Results of this study suggest some improvements for the management of deer population in the landscape. Since the use of seasonal ranges is traditional, parameters such as the distance and direction of migration, and the locations of connected summer and winter ranges are predictable. Migration timing is largely a function of weather conditions and is predictable as well (Nelson 1995).

The population dynamics of northern deer are largely controlled by hunting mortality which is, in turn, under the control of the managers who set regulations. Managers might assert greater control over a region's deer population by 1) designating biologically meaningful deer management units based on pairs of winter and summer ranges which are connected in the landscape by deer migration tradition, and 2) abandoning the predominantly bucks-only harvest regulations.

Modeling of potential deeryards in relation to the intensity of deer use should continue because it would allow managers objective means for identifying potential deeryards across the landscape. The deeryard boundaries used in this study were based on the subjective opinions of MDNR managers familiar with the area. Ideally models should be able to differentiate between conifer swamp areas that are used as deeryards and those that are not.

Habitat modeling, mortality rates, and migration characteristics should be used to examine interactions between deeryards and the surrounding matrix of summer range in terms of seasonal deer distributions. Presumably some deeryards are less important to the summer distribution of deer because of the proximity of other deeryards. The less important ones may be good candidates for regeneration and herd reduction experiments. This same information could be incorporated into spatially-explicit population models useful for examining the meta-population dynamics of northern deer. Obtaining movement information need not be expensive if conservationist clubs supply volunteers and supplies. The cooperation of UP Whitetails and their trap-tag-release programs should serve as a model for managers and sportsmen from throughout the region.

Reductions in deer densities in a given yard are likely to affect the distribution of deer on the surrounding summer range. Movement tradition could be used to predict these effects. The rate at which "holes" in the summer range distribution can be recolonized as new movement traditions develop needs to be further evaluated. A shift towards more antlerless hunting may speed recolonization rates by disrupting migration tradition. More orphaned fawns would be forced to seek out unoccupied ranges and new traditions would be formed.

APPENDIX

Table 13. Sex, age, movement, and fates of radio-collared deer in Michigan's Upper Peninsula.

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
F	Adult	20 Jan. 1992	M	Killed by coyotes 26 Apr. 1993
F	Adult	20 Jan. 1992	N	Killed on crop damage permit 23 Aug. 1992
F	Adult	20 Jan. 1992	M	Dead 12 June 1992 cause unknown
F	151	20 Jan. 1992	N	Dead 27 Jul. 1993, cause unknown
M	7	21 Jan. 1992	N	Killed by hunters 13 Oct. 1992
F	Adult	21 Jan. 1992	M	Killed by unknown predator 23 Feb. 1994
M	7	21 Jan. 1992	M	Killed by coyotes 30 Apr. 1992
F	Adult	22 Jan. 1992	N	Killed by unknown predator 28 May 1992

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
M	7	27 Jan. 1992	N	Killed by bear 1 Sept. 1992
F	7	27 Jan. 1992	M	Dead 30 Apr. 1992 (cause unknown)
M	7	27 Jan. 1992	U	Dead 11 April 1992, starvation
M	7	28 Jan. 1992	N	Killed by hunter 19 Nov. 1992
F	19	28 Jan. 1992	M	Censored 21 July 1994 (dead battery)
M	7	29 Jan. 1992	N	Bear predation 22 July 1992
F	7	29 Jan. 1992	M	Censored 25 Jan. 1994 (dead battery)
M	7	29 Jan. 1992	M	Killed by hunter 18 Nov. 1992
M	19	30 Jan 1992	N	Killed by hunter 15 Dec. 1992

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
M	19	30 Jan. 1992	M	Killed by hunter 24 Nov. 1992
F	Adult	1 Feb. 1992	M	Alive
F	Adult	5 Feb. 1992	N	Alive
F	Adult	5 Feb. 1992	N	Alive
M	20	11 Feb. 1992	N	Killed by hunter 15 Nov. 1992
M	32	16 Feb. 1992	M, I	Killed by hunter 15 Nov. 1993
M	Adult	18 Feb. 1992	M	Died 27 Apr. 1994, cause unknown
F	Adult	27 Feb. 1992	N	Alive
F	8	29 Feb. 1992	N	Censored 28 Feb. 1994 (dead battery)
F	9	2 Mar. 1992	M	Censored 31 Aug. 1993 (dead battery)
F	97	2 Mar. 1992	N	Alive
M	9	3 Mar. 1992	N	Starvation 28 May 1992

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
M	9	3 Mar. 1992	A	Censored 15 Dec. 1994 (dead battery)
F	9	4 Mar. 1992	M	Censored 15 Feb. 1993 (Collar malfunction)
F	9	5 Mar. 1992	U	Starvation 30 Mar. 1992
M	9	5 Mar. 1992	N	Killed by hunter 22 Oct. 1992
F	Adult	6 Mar. 1992	M	Alive
F	9	11 Mar. 1992	M	Killed by bear 5 May 1992
F	Adult	11 Mar. 1992	N	Censored/radio failure - sporadic sightings 1992-1994
F	153	12 Mar. 1992	M	Killed by wolves 22 Apr. 1993
F	45	12 Mar. 1992	M,I	Alive
F	9	13 Mar. 1992	M	Dead 19 May 1992 cause unknown
F	7	28 Jan. 1993	M	Censored 27 Jul. 1994 (collar malfunction)

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
F	Adult	28 Jan. 1993	M	Alive
F	7	28 Jan. 1993	U	Poached 16 May 1994
F	7	28 Jan. 1993	N	Dead 8 Sept 1994 Hit by car.
M	7	28 Jan. 1993	N	Dead 14 Oct. 1993 cause unknown
M	7	28 Jan. 1993	N	Dead 31 Aug. 1993 cause unknown
M	7	28 Jan. 1993	M	Dead 12 Nov. 1993 cause unknown
F	115	29 Jan. 1993	A	Dead 7 Jun. 1994 cause unknown
F	7	29 Jan. 1993	A	Alive
F	223	29 Jan. 1993	M	Dead 20 Apr. 1994, cause unknown
F	7	30 Jan. 1993	A	Killed by unknown predator 12 Jun. 1994
M	7	30 Jan. 1993	M,I	Killed by hunter 17 Nov. 1994

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
M	8	4 Feb. 1993	N	Dead 21 Oct. 1993 cause unknown
M	20	10 Feb. 1993	M	Killed by hunter 15 Nov. 1993
F	8	10 Feb. 1993	M	Alive - Killed by a bobcat 9 Jan. 1995
M	8	10 Feb. 1993	M	Killed by hunter 9 Dec. 1993
M	8	10 Feb. 1993	N	Killed by hunter 29 Oct. 1993
F	8	10 Feb. 1993	N	Alive
F	8	11 Feb. 1993	N	Censored 23 June 1993 (slipped collar)
M	8	12 Feb. 1993	M	Killed by hunter 19 Nov. 1993
M	20	13 Feb. 1993	N	Killed by hunter 3 Dec. 1994
M	20	14 Feb. 1993	M	Dead 3 Jan. 1994, possible crippling loss

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
F	140	26 Feb. 1993	M	Poached 22 Nov. 1993
F	176	26 Feb. 1993	M	Alive
M	21	7 Mar. 1993	N	Killed by hunter 19 Nov. 1993
F	69	8 Mar. 1993	N	Alive
F	9	8 Mar. 1993	N	Alive
M	9	11 Mar. 1993	M	Killed by hunter 11 Nov. 1994
M	9	13 Mar. 1993	U	Starvation 6 Apr. 1993
F	153	13 Mar. 1993	M,I	Censored 19 Apr. 1994
F	9	16 Mar. 1993	M,I	Censored 27 Sept 1994
F	21	19 Mar. 1993	N	Alive
F	9	19 Mar. 1993	M?, I?	Censored 27 Aug. 1993 possible dispersal
M	8	26 Feb. 1993	M?	Alive - Possible dispersal
M	7	14 Jan. 1994	M	Alive
F	7	15 Jan. 1994	N	Alive
F	7	22 Jan. 1994	N	Killed by hunter 26 Nov. 1994
M	7	23 Jan. 1994	N	Dead 22 June cause unknown

Table 13 (cont'd)

Sex	Age at Capture (months)	Date of Capture	Movement[a]	Fate
M	7	23 Jan. 1994	N	Killed by hunter 23 Nov. 1994
F	7	23 Jan. 1994	N	Alive
M	7	25 Jan. 1994	N	Alive
M	7	27 Jan. 1994	M	Starvation 27 Apr. 1994
M	8	9 Feb. 1994	U	Starvation 11 Apr. 1994
M	8	11 Feb. 1994	N	Killed by hunter 30 Oct. 1994
M	8	11 Feb. 1994	M	Alive
F	8	14 Feb. 1994	M	Dead 20 Apr. 1994 (cause unknown)
F	8	21 Feb 1994	M,I	Alive
F	8	23 Feb 1994	M	Alive
M	8	26 Feb. 1994	U	Killed by bobcat or coyote 11 Apr. 1994
F	8	28 Feb. 1994	N	Alive
F	9	1 Mar. 1994	M	Alive
F	9	28 Mar. 1994	U	Killed by coyotes

[a] M = migratory, N = non-migratory, U = unknown, A = ambiguous, I = use of intermediate range

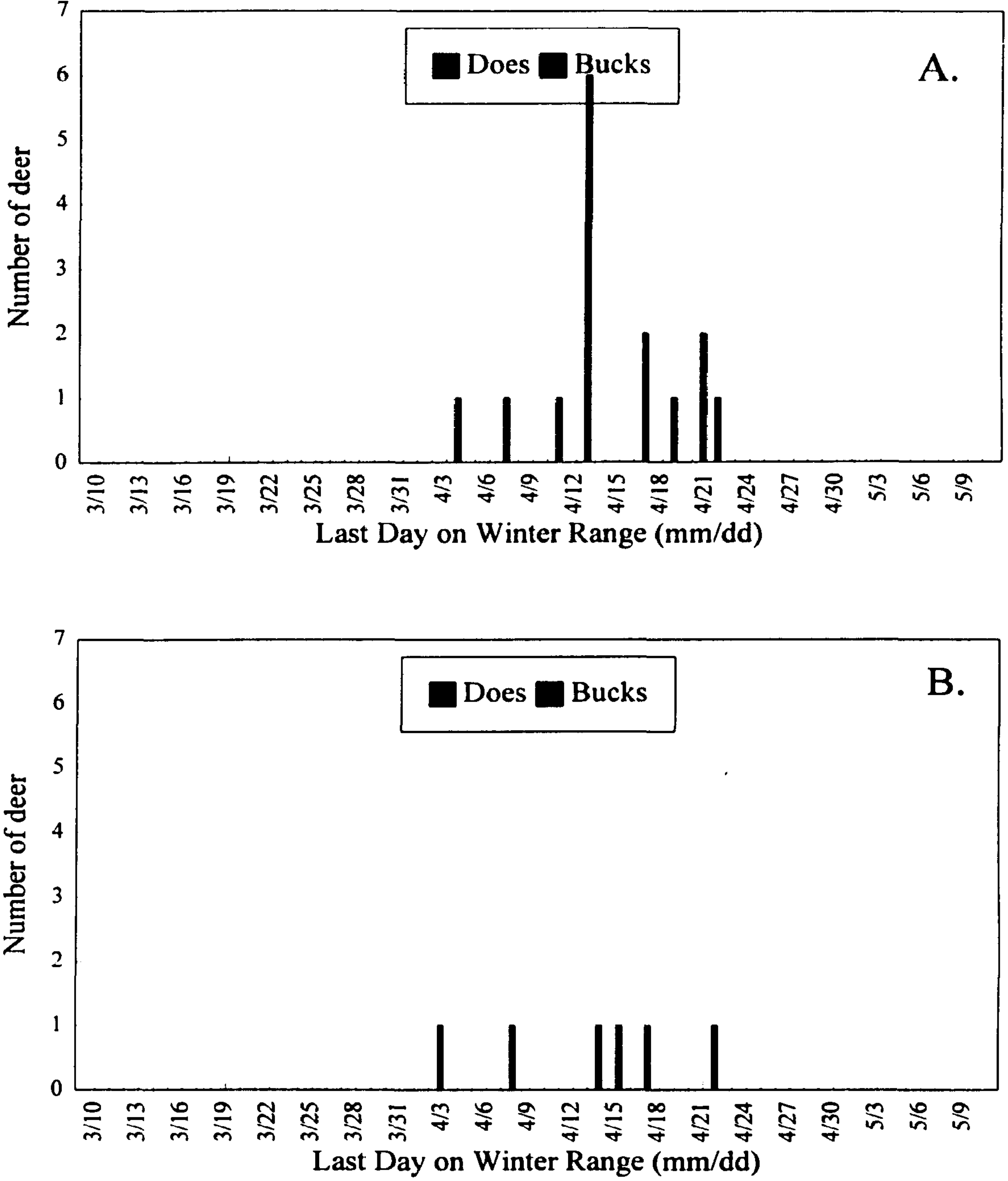


Figure 23. Distribution of 1992 last days on the deeryard for migratory radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.

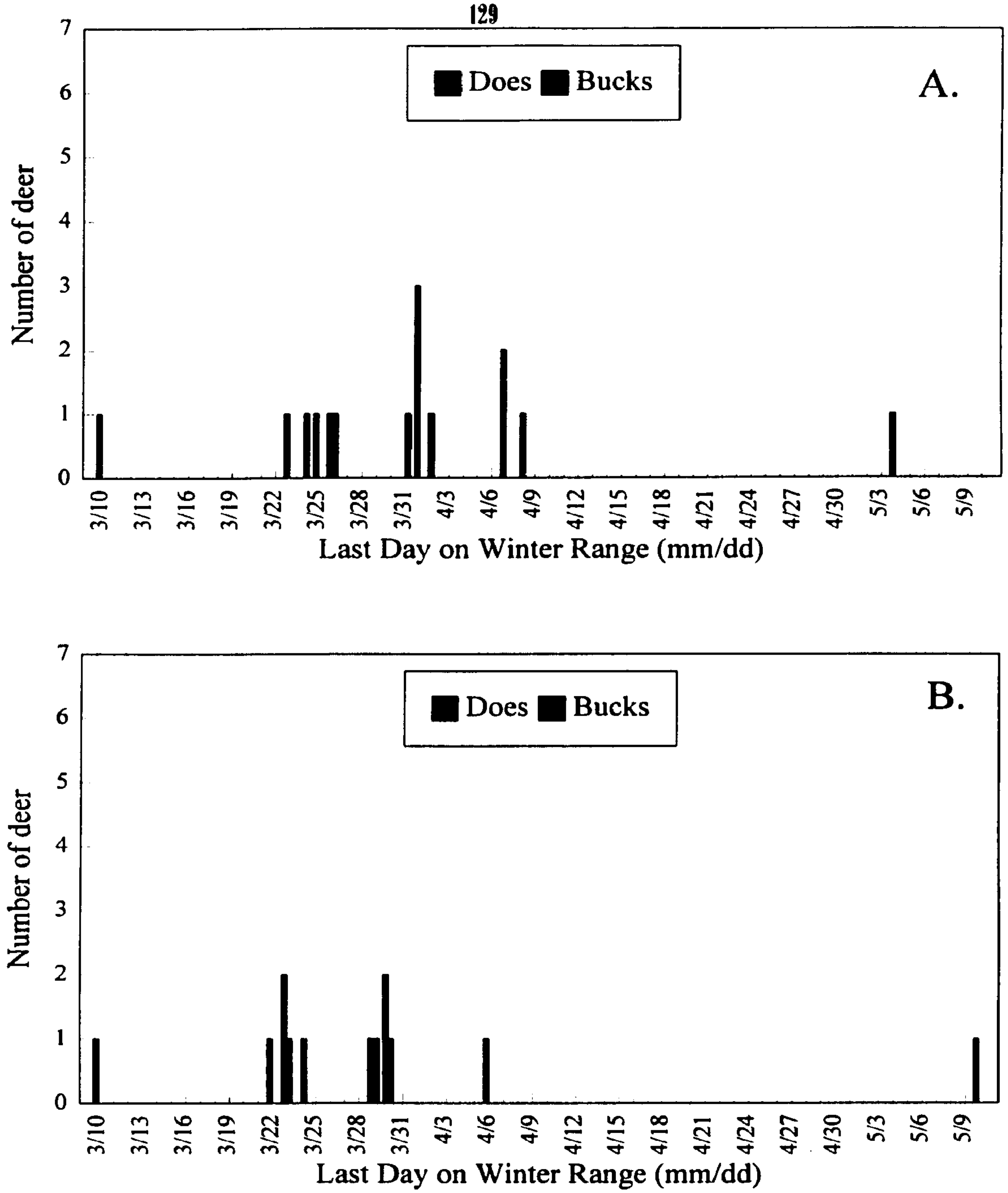


Figure 24. Distribution of 1993 last days on the deeryard for migratory radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.

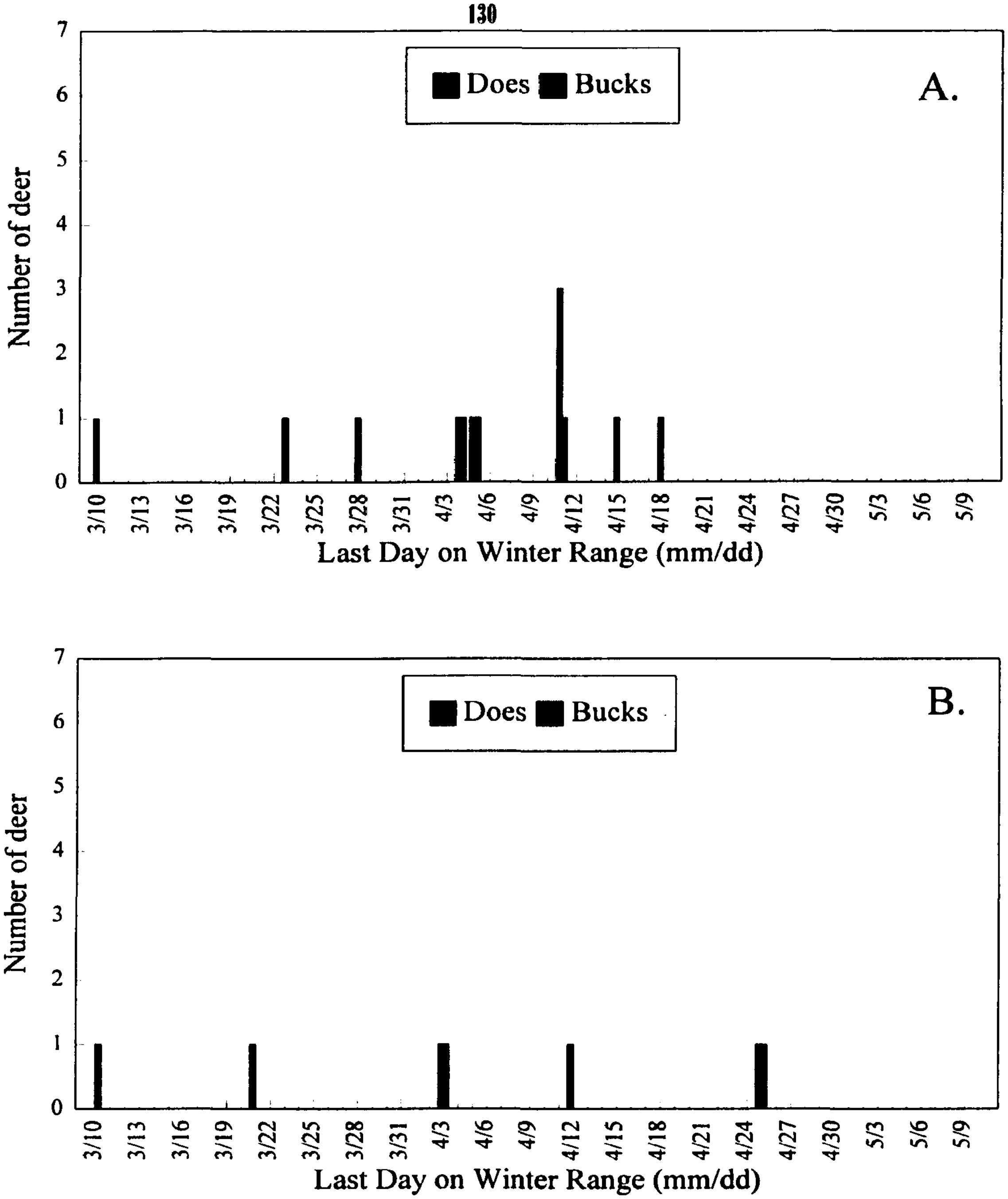
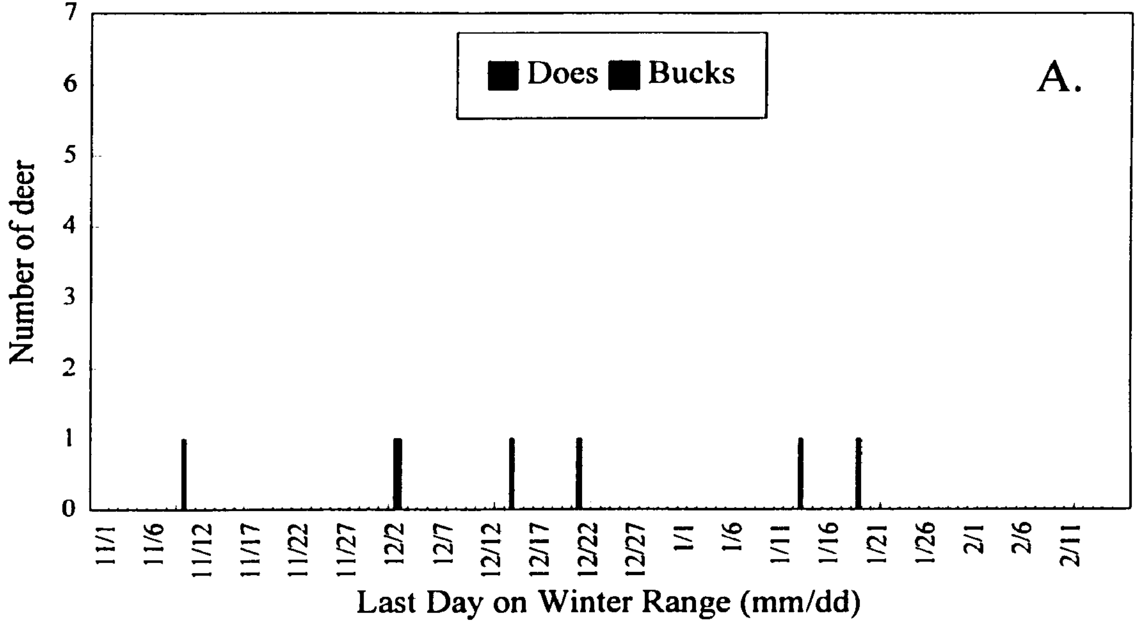


Figure 25. Distribution of 1994 last days on the deeryard for migratory radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.



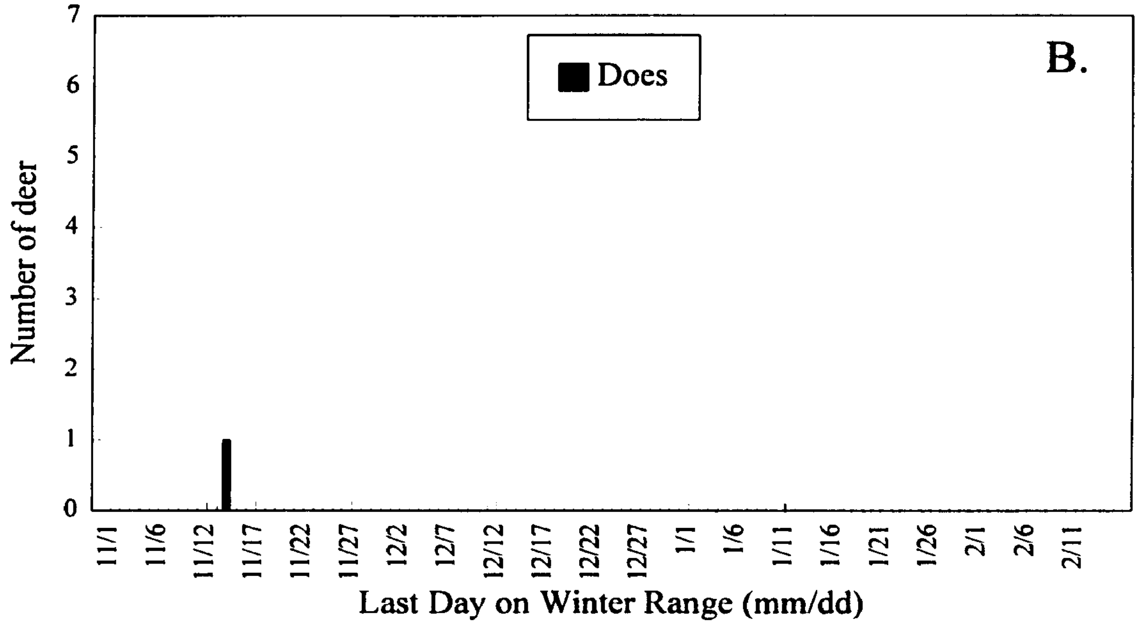
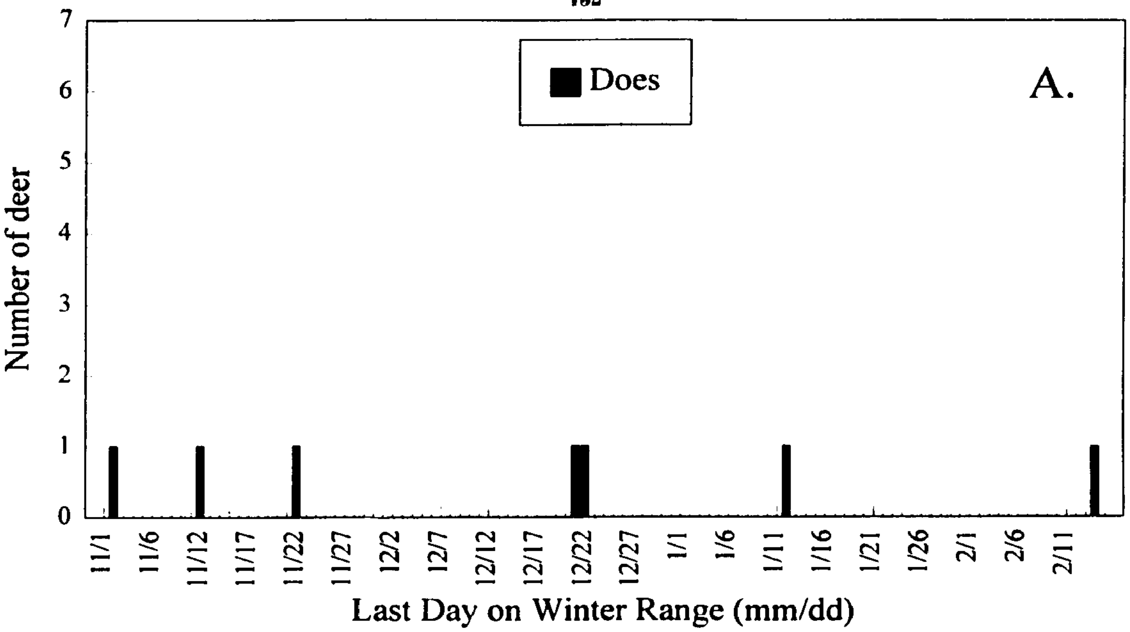


Figure 26. Distribution of 1992 - 1993 last days on the summer range for migratory radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.



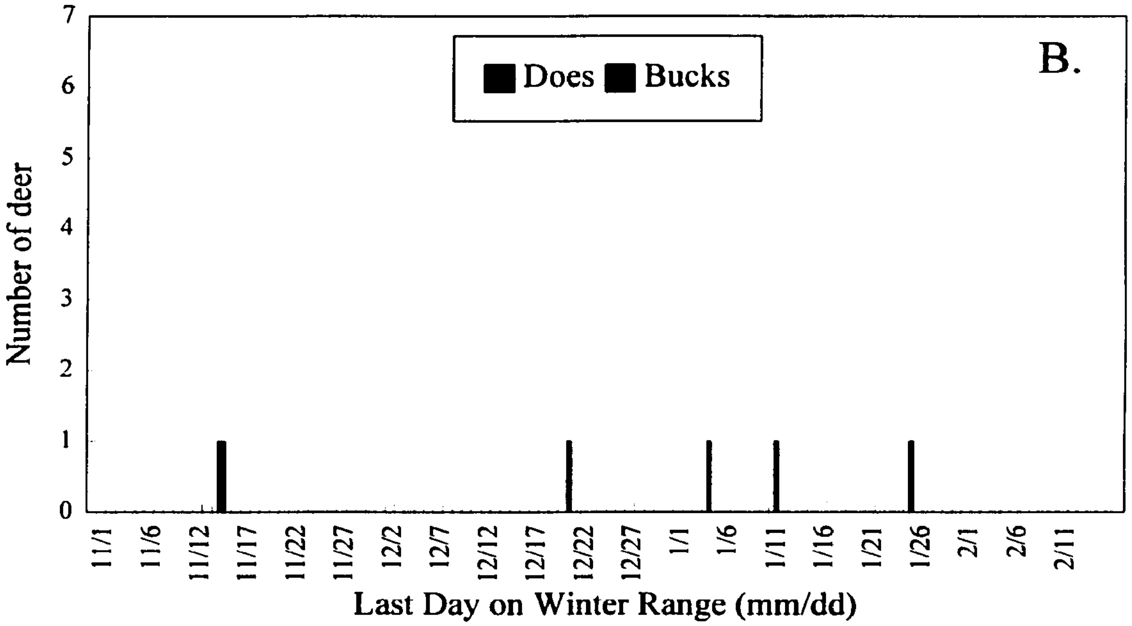
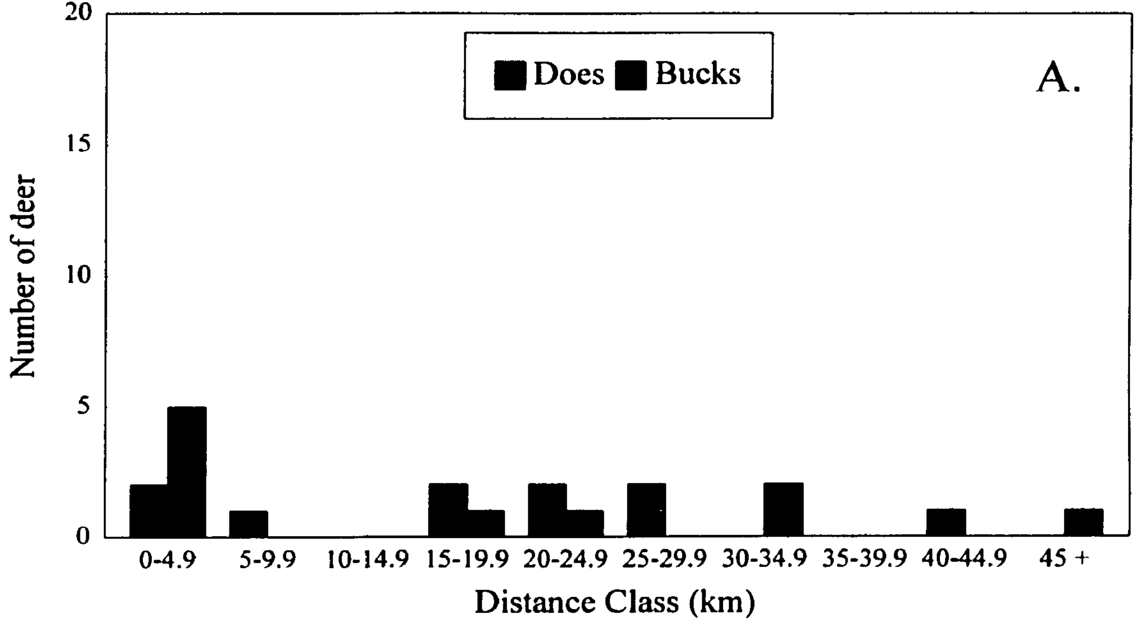


Figure 27. Distribution of 1993 - 1994 last days on the summer range for migratory radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.



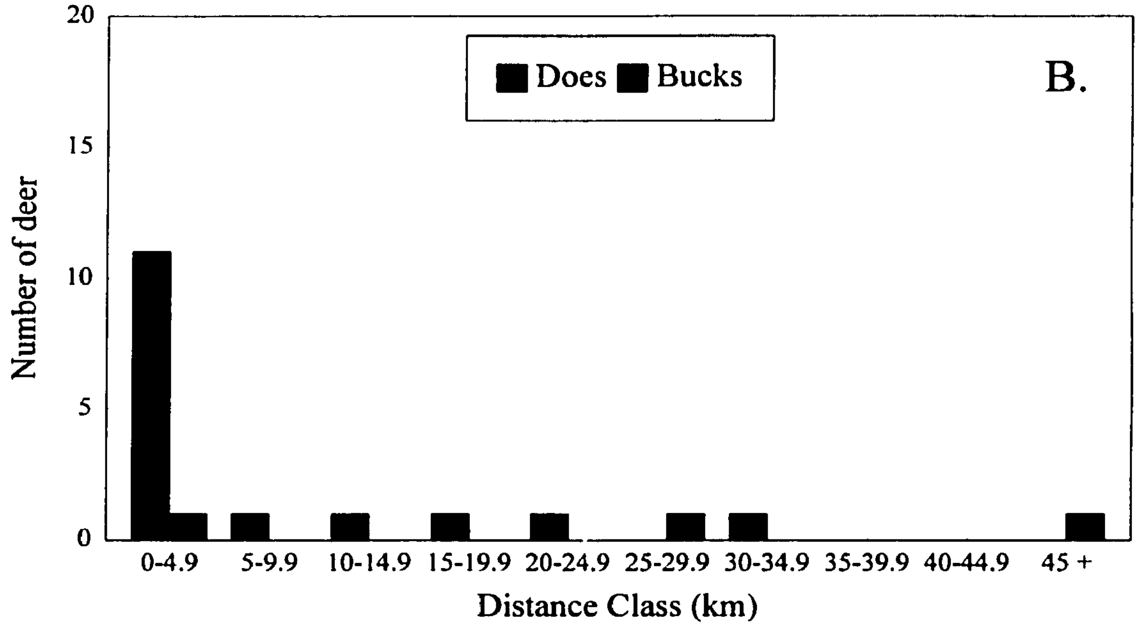
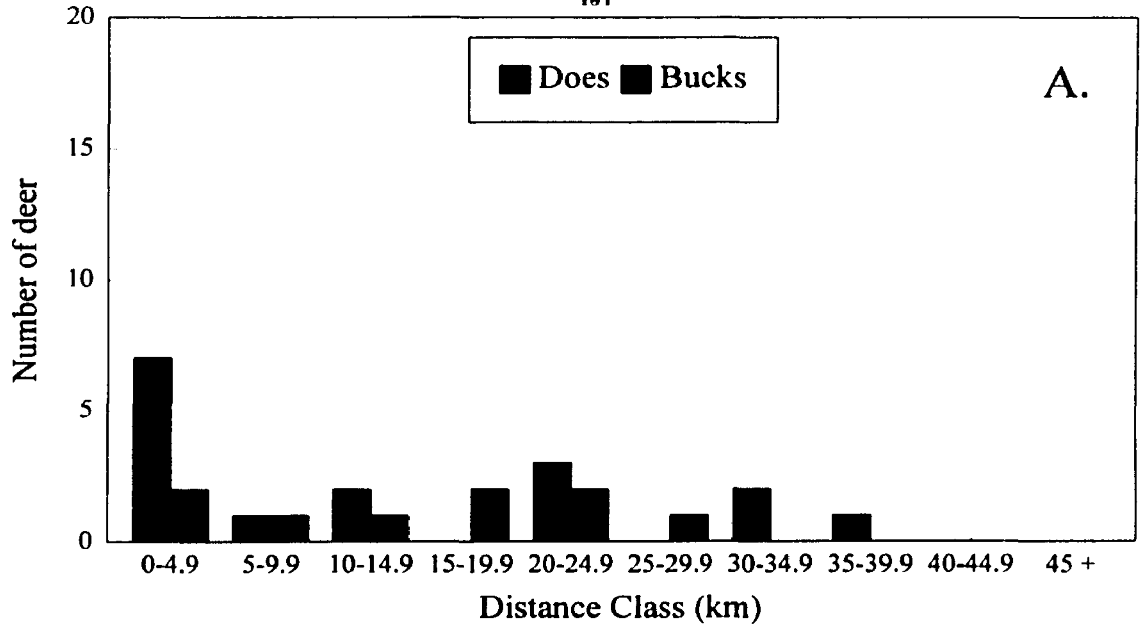


Figure 28. Distribution of spring 1992 migration distances for radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.



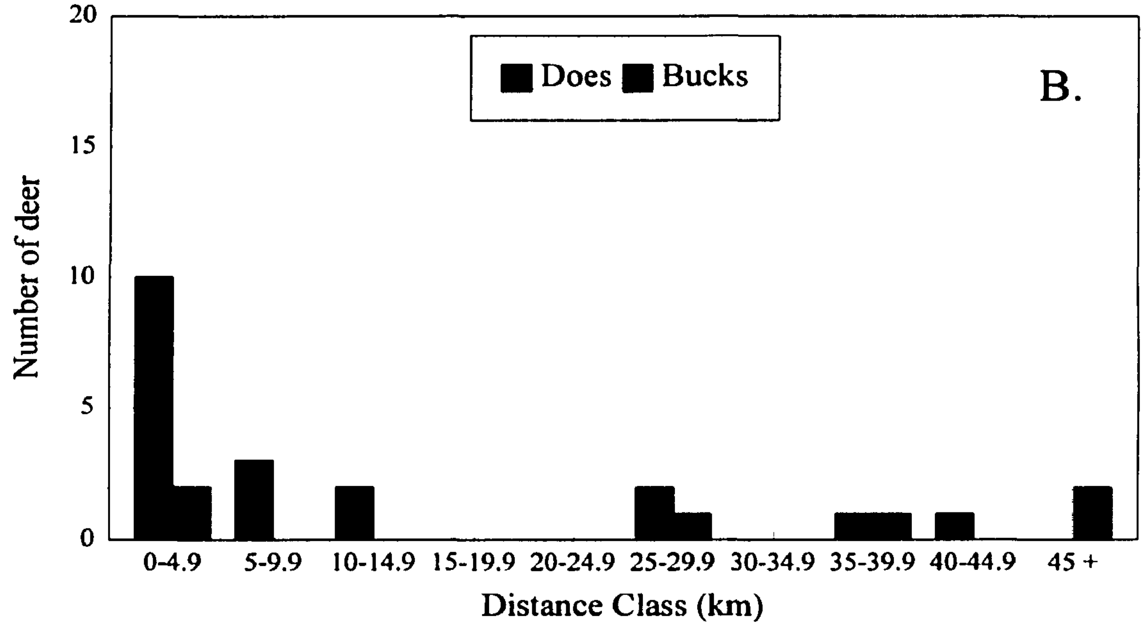


Figure 29. Distribution of spring 1993 migration distances for radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.

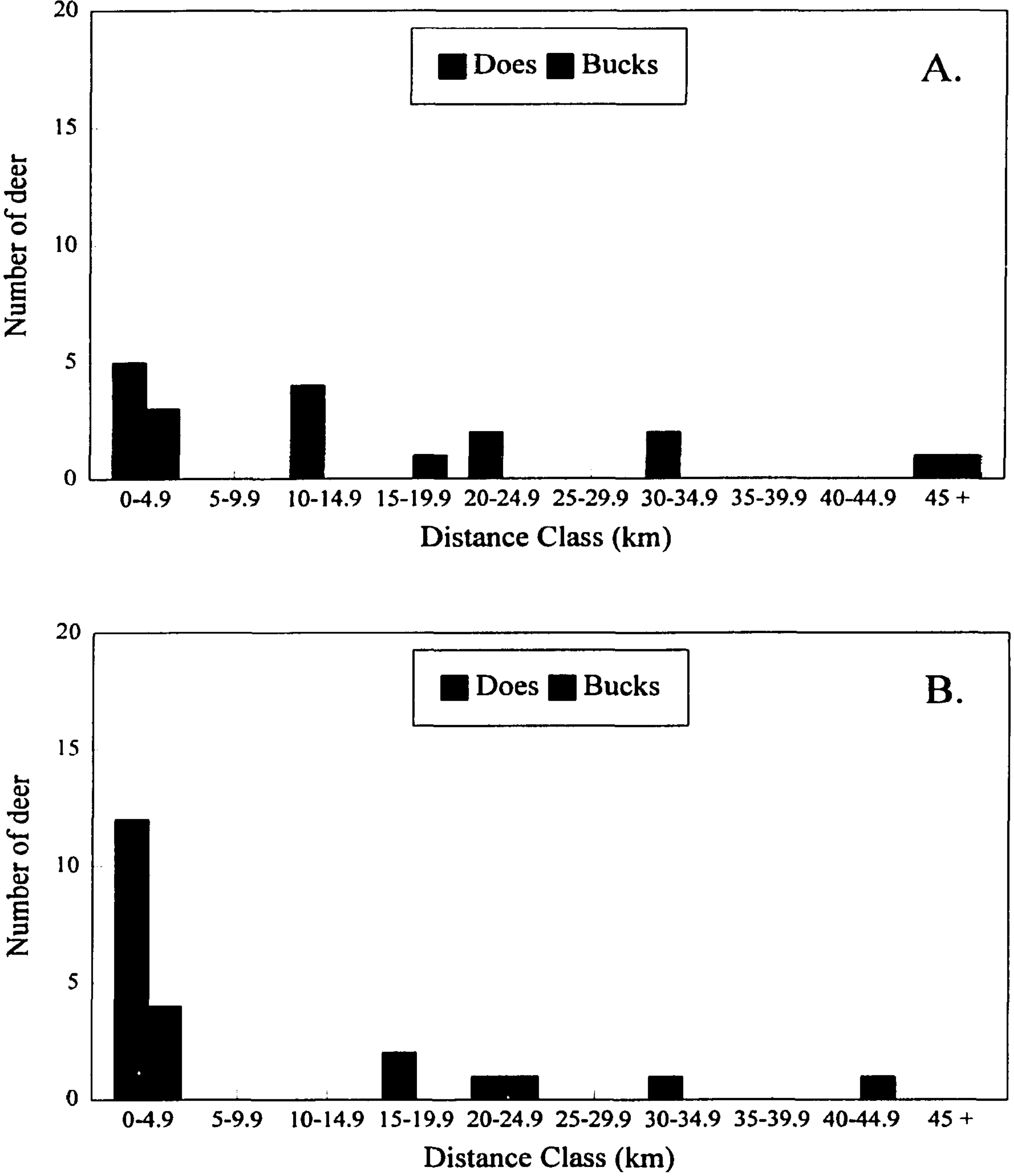
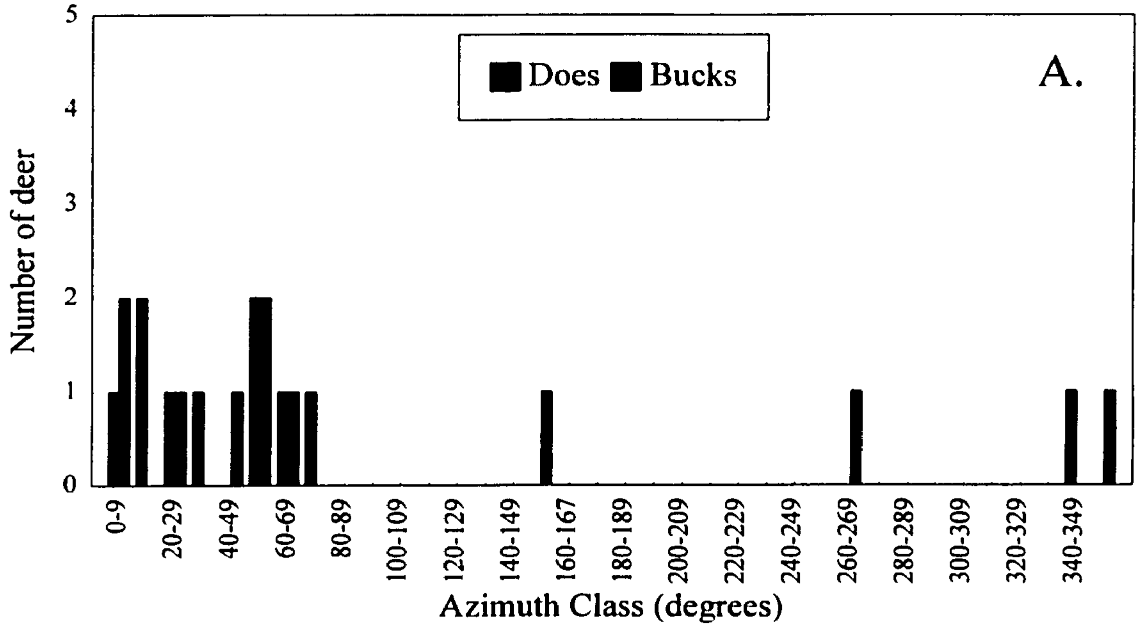


Figure 30. Distribution of spring 1994 migration distances for radio-collared deer that winter on the Whitefish (A.) and Stonington (B.) deeryards.



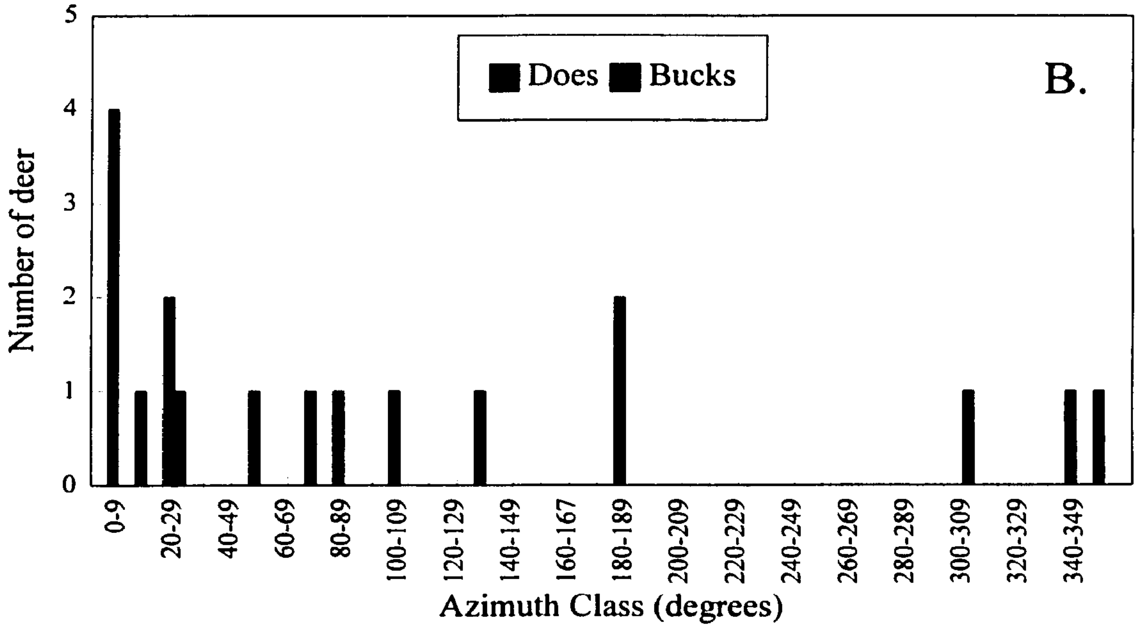
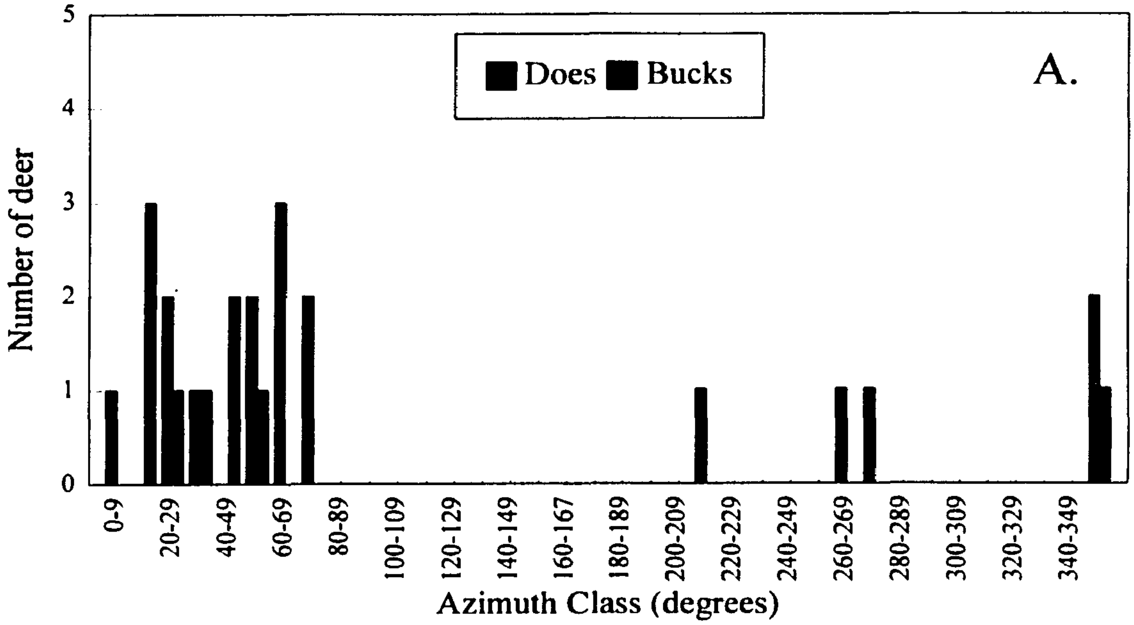


Figure 31. Directions of spring 1992 migrations for radio-collered deer using the Whitefish (A.) and Stonington (B.) deeryards.



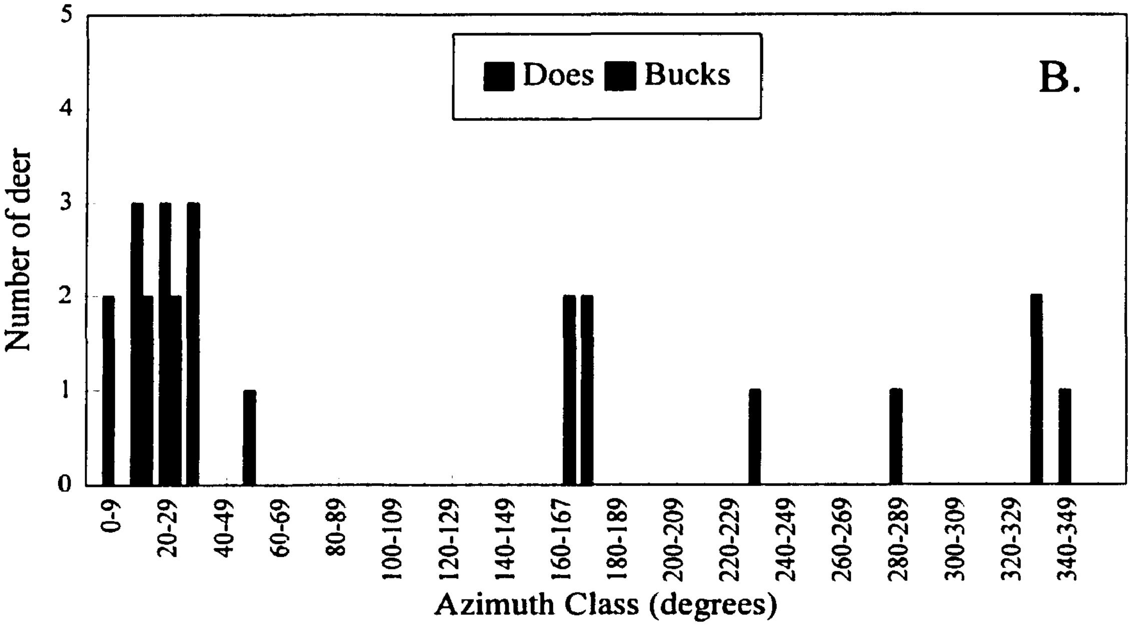


Figure 32. Directions of spring 1993 migrations for radio-collered deer using the Whitefish (A.) and Stonington (B.) deeryards.

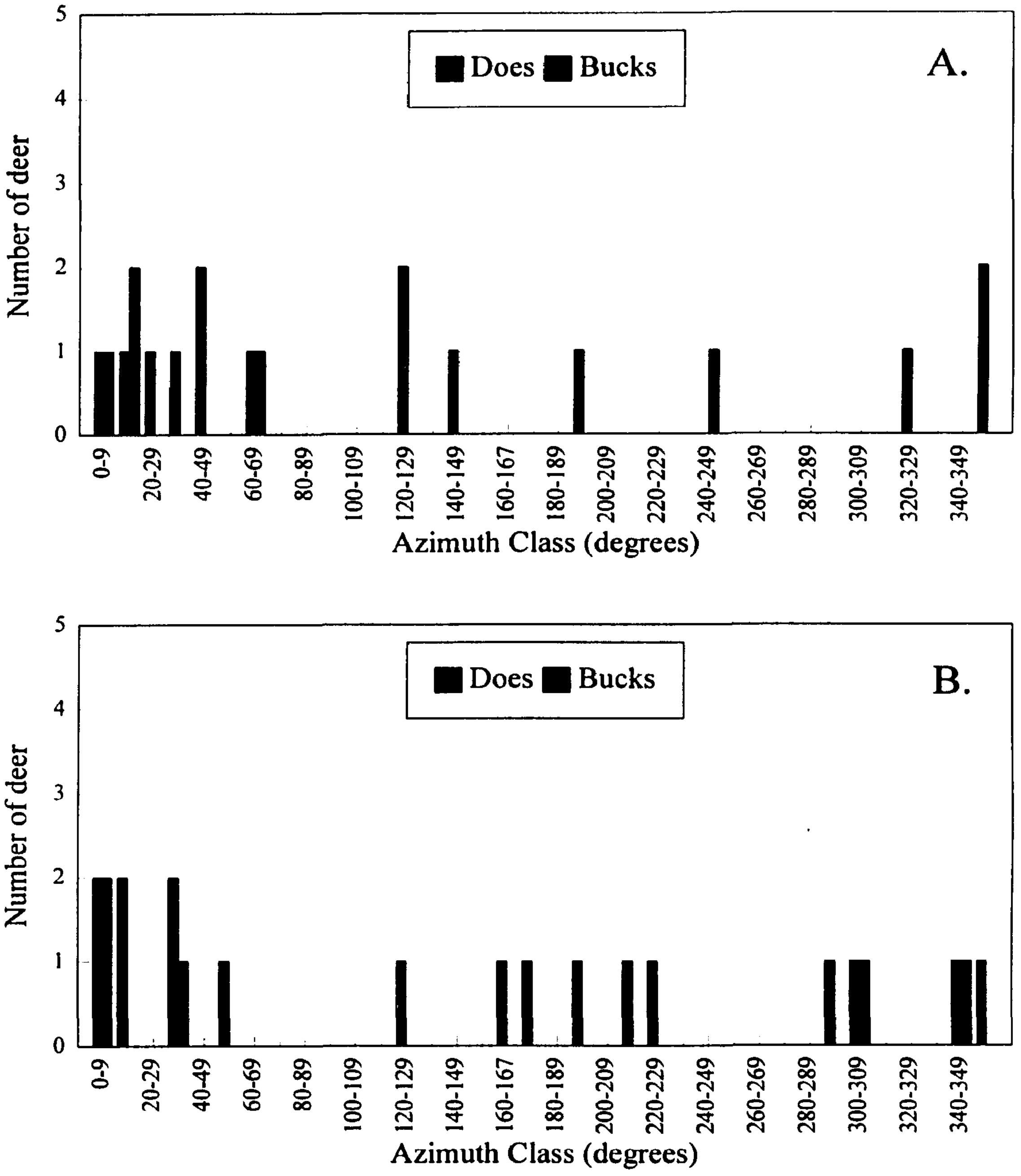
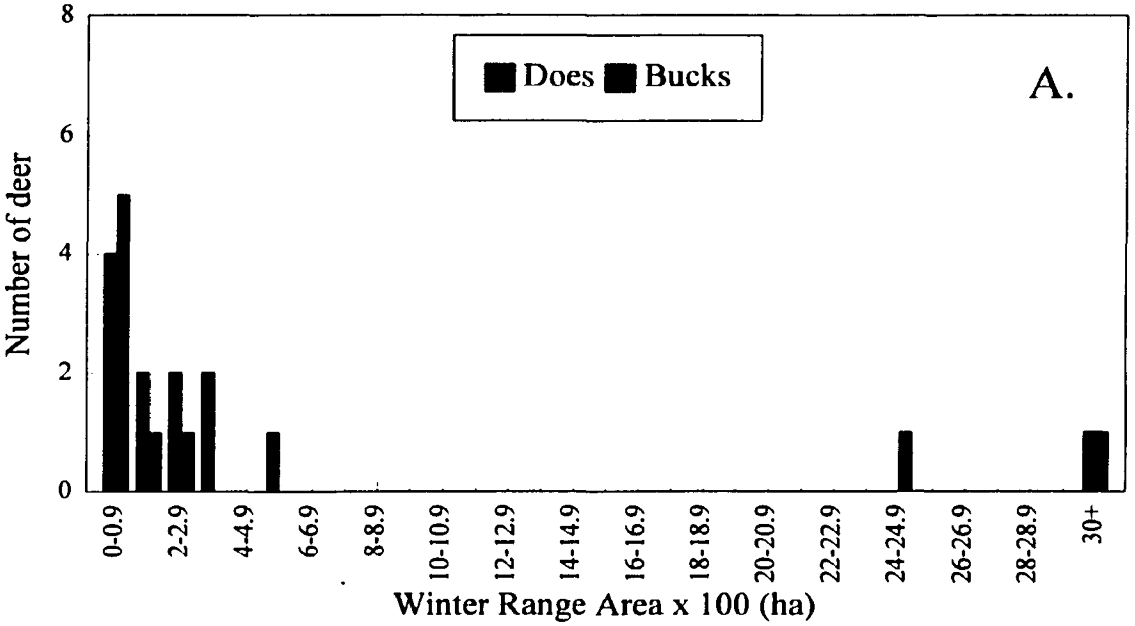


Figure 33. Directions of spring 1994 migrations for radio-collered deer using the Whitefish (A.) and Stonington (B.) deeryards.



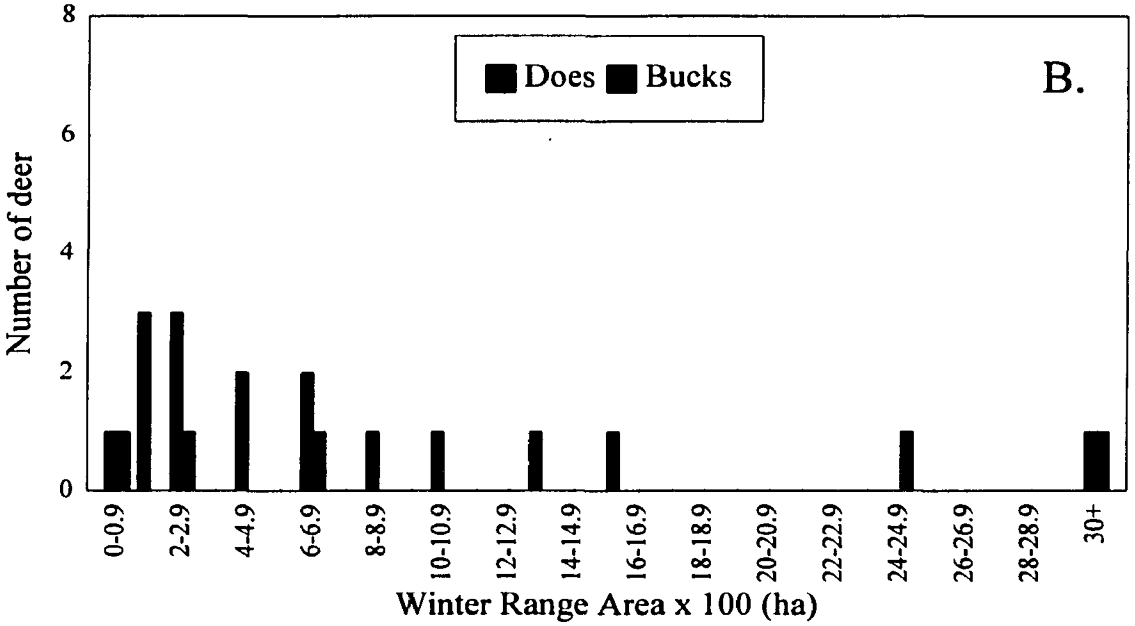
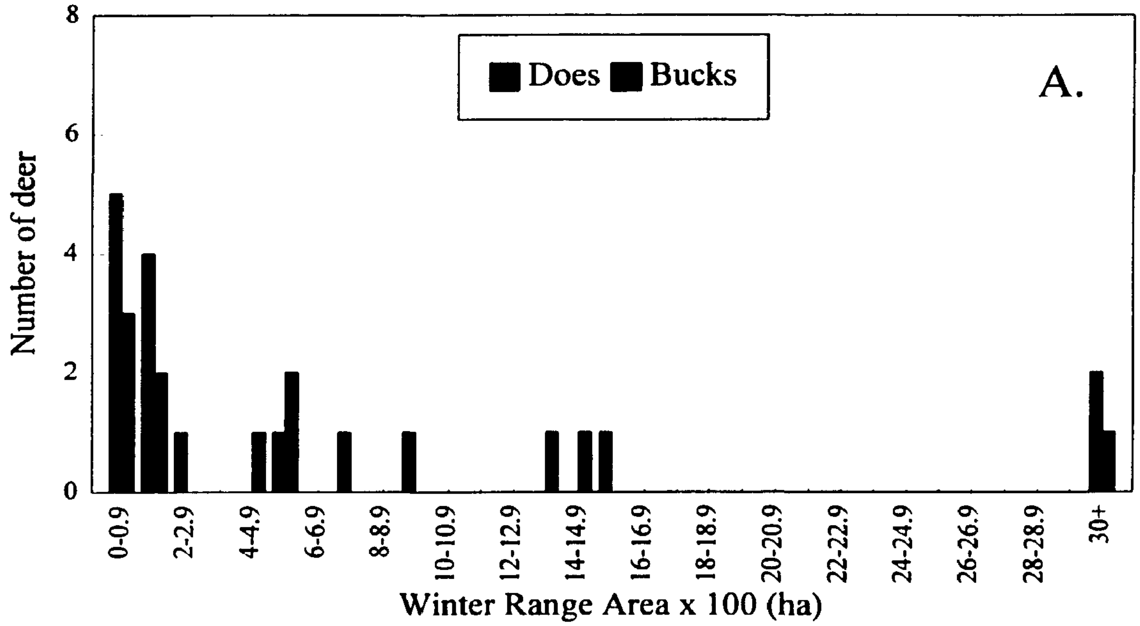


Figure 34. Winter range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1992. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).



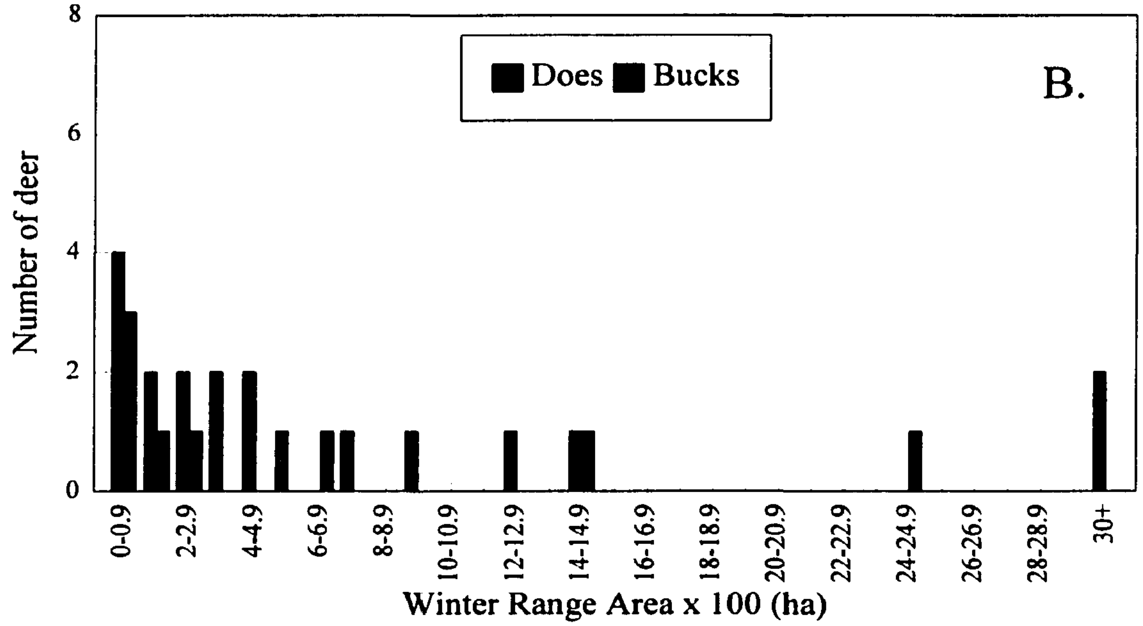
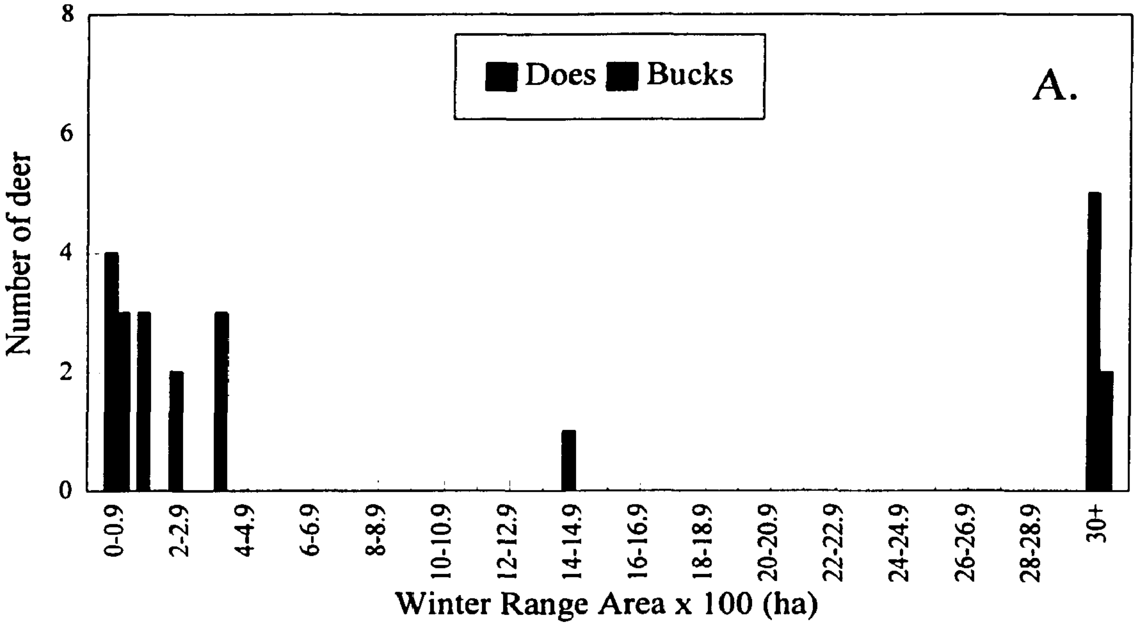


Figure 35. Winter range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1993. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).



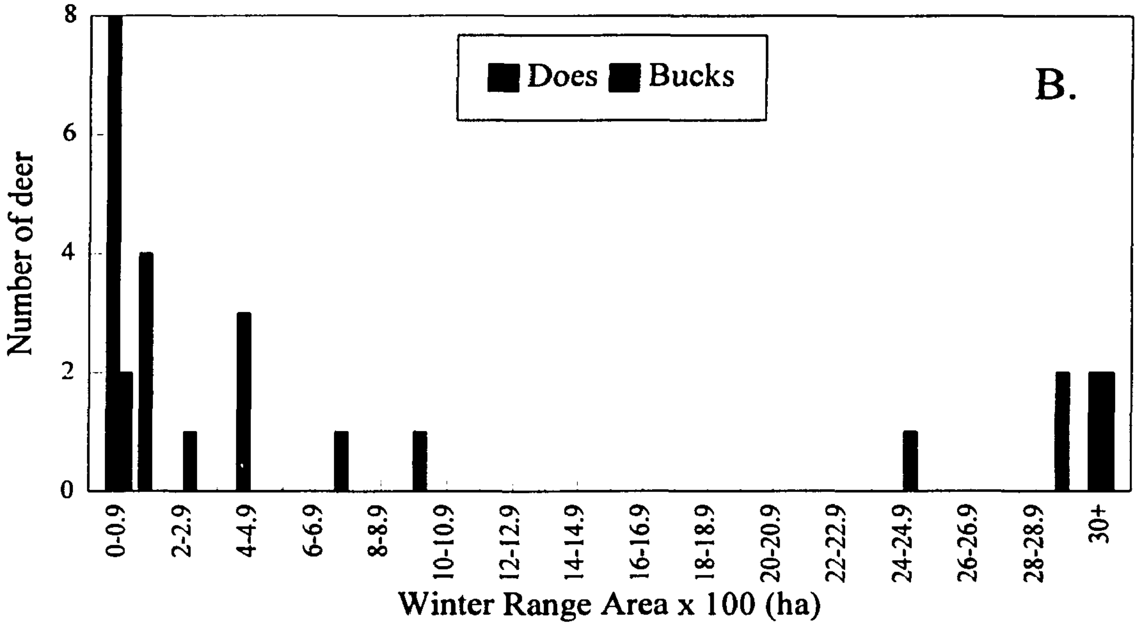


Figure 36. Winter range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1994. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).

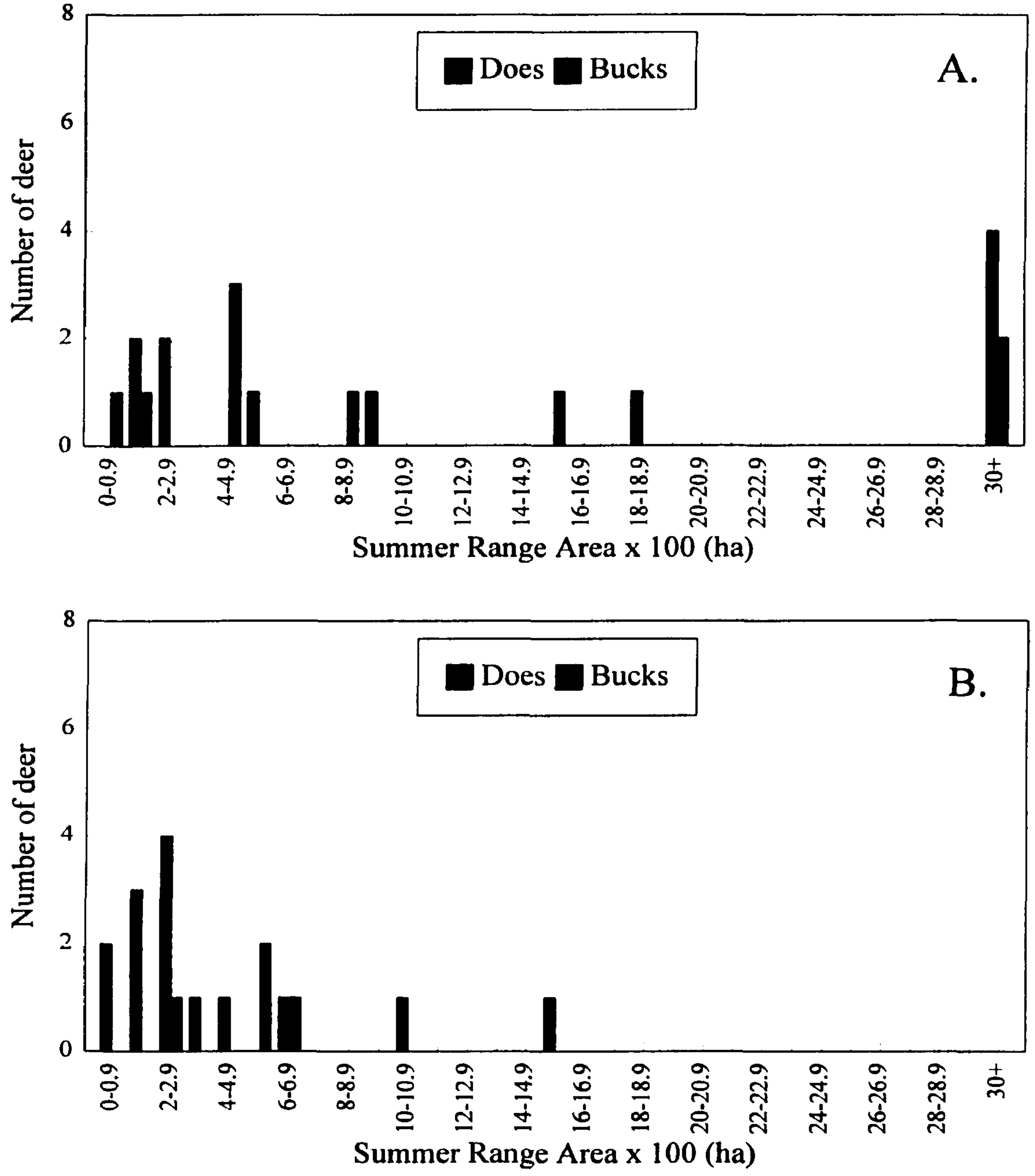


Figure 37. Summer range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1992. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).

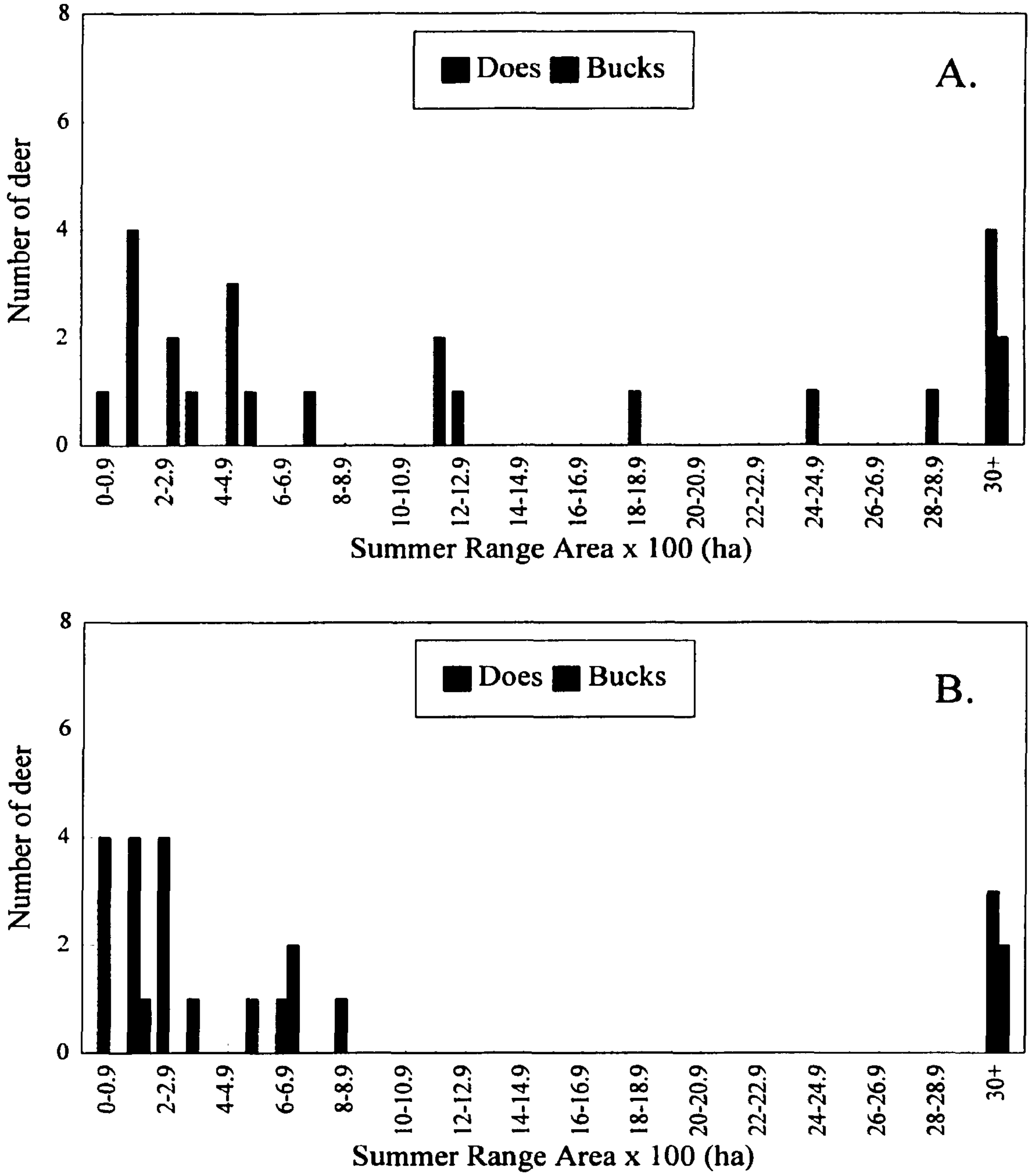
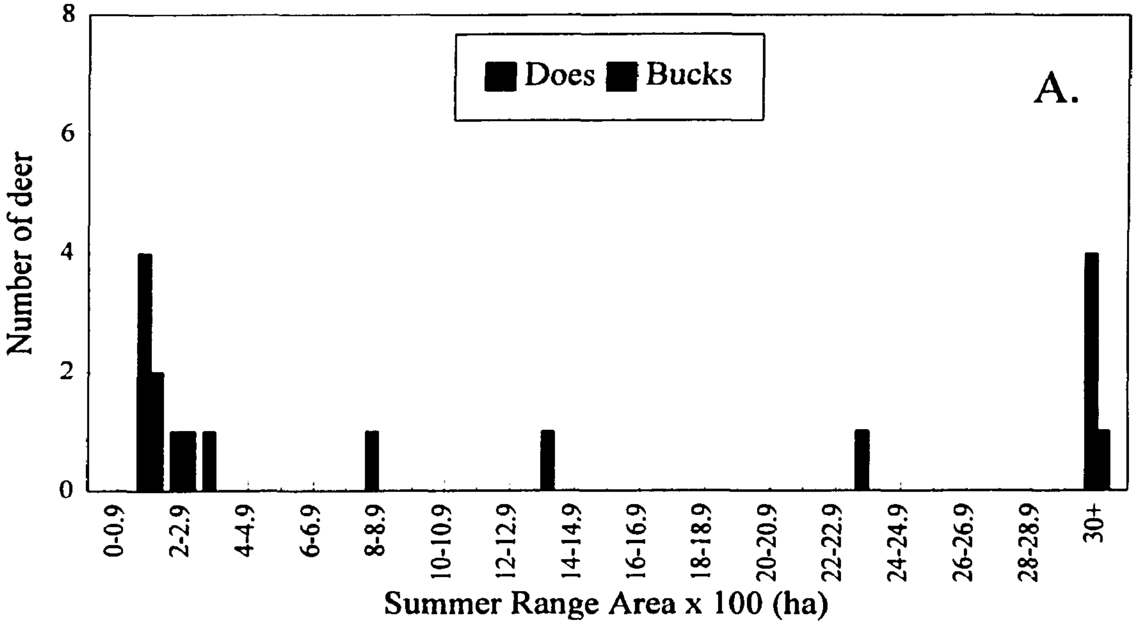


Figure 38. Summer range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1993. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).



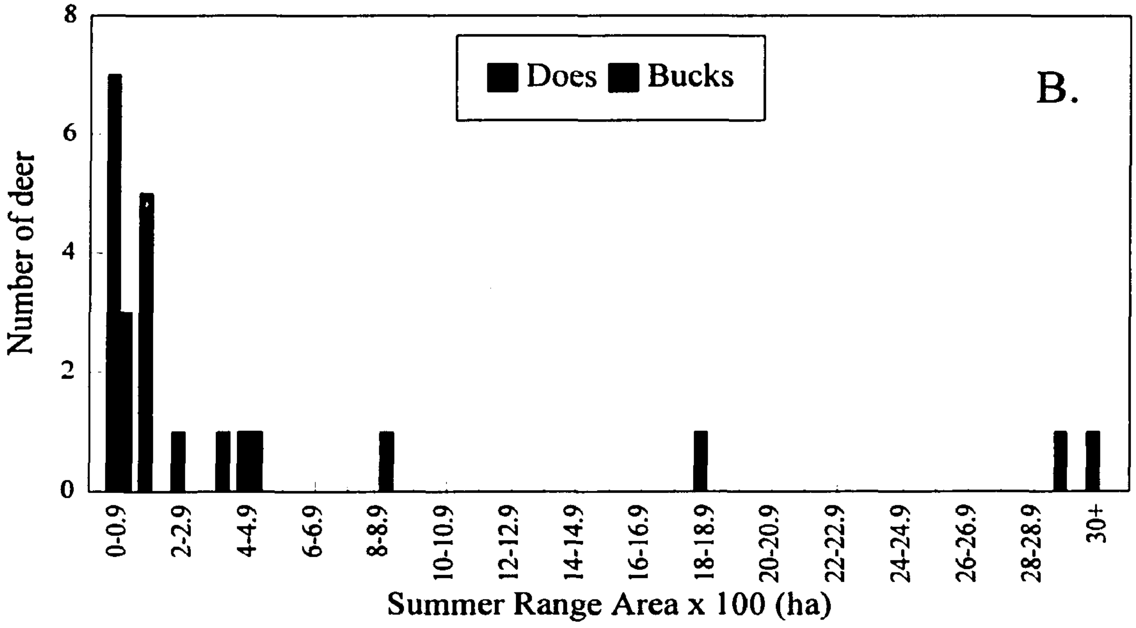


Figure 39. Summer range areas for radio-collared deer using the Whitefish (A) and Stonington (B) deeryards in 1994. Areas were calcualted from the 95% Adaptive Kernal contours (Worton 1989).

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