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DEER MANAGEMENT IN ONTARIO (1980-1997): IMPLICATIONS FOR FUTURE MANAGEMENT

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Abstract

The Ontario of Ministry Natural Resources spends considerable effort each year managing white-tailed deer (*Odocoileus virginianus*). A selective harvest system, which regulates kill by issuing a restricted number of either-sex harvest permits (called tags), has been the main tool employed to manage populations. Using harvest and biological data from 1980 to 1997, we reviewed the historical ability to regulate both harvest and population size in Ontario, and assessed our ability to predict future population size. Under the selective harvest system, when more than 40% of hunters hold tags, kill can only be significantly increased by increasing hunter numbers and even below 40% tags, the most effective regulation of kill involves regulating both the number of tags and the number of hunters. The ability to regulate harvest may also be limited by hunter behaviour. Deer population size, as indicated by deer seen controlling for effort, was mainly regulated by density-dependence, with limited effects from summer and winter weather conditions. Harvest exhibited no effect on population size, except in a few, select areas where relatively large kills produced limited down-regulation. The best model created to predict changes in population, for management purposes, had poor predictive ability and barely outperformed randomly choosing a number. These results indicate an inability to regulate deer populations through a sport harvest. Kill, at historical levels, does not appear to regulate population density. Further, based on currently collected data, we are unable to make accurate predictions of future population size on which to base management decisions. We suggest a new management system, in recognition of the limited predictive and management ability, in which management actions are untaken only when estimated populations exceed broad limits.

Résumé

Le ministère des Ressources naturelles de l'Ontario met des efforts considérables chaque année pour gérer les populations de Cerf de Virginie (*Odocoileus virginianus*). Un système de récolte sélective, qui réglemente la mortalité en émettant un nombre limité de permis de chasse pour l'un ou l'autre des deux sexes, a été le principal outil employé pour gérer les populations de cerfs en Ontario. En utilisant des données sur les récoltes et les caractéristiques biologiques des populations de cerf pour la période de 1980 à 1997, nous avons évalué, d'une part, la capacité historique du ministère à réglementer les récoltes et la taille des populations de cerf en Ontario et, d'autre part, notre aptitude à prédire la taille future des populations de cerf. Avec le système de récolte sélective, lorsque plus de 40% des chasseurs détiennent un permis, la seule façon d'accroître significativement la mortalité est d'augmenter le nombre de chasseurs. Avec moins de 40% de détenteurs de permis, le contrôle le plus efficace de la mortalité consiste à réglementer à la fois le nombre de permis et le nombre de chasseurs. Toutefois, la capacité à réglementer la récolte peut aussi être sujette au comportement des chasseurs. La taille des populations de cerf, tel qu'indiquée par le nombre de cerf aperçu (contrôlé pour l'effort), fut principalement contrôlée par la densité, avec peu d'effet des conditions météorologiques en été et hiver. Les récoltes n'eurent aucun effet sur la taille des populations, sauf dans quelques régions où des mortalités relativement importantes ont produit une régulation à la baisse, bien que limitée, des populations. Le modèle pouvant le mieux prédire les changements au sein des populations de cerf fut caractérisé par une faible capacité de prédiction, et à peine surpassait le choix aléatoire d'un numéro. Ces résultats indiquent une incapacité à réglementer les populations de cerfs au moyen des récoltes sportives. La mortalité, à des niveaux historiques, ne semble pas contrôler la densité des populations. De plus, en se basant sur les données actuellement récoltées, nous sommes incapables de prédire de façon juste la taille future des populations de cerf, sur laquelle baser les décisions de gestion. Reconnaissant la capacité limitée de prédiction et gestion des populations de cerf, nous suggérons un nouveau système de gestion avec lequel des actions de gestion seraient entreprises seulement lorsque la taille estimée de la population excèderait des limites établies à des niveaux élevé ou faible, selon le cas.

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Chapter 1: Deer management background and data descriptions.

1. Deer management in Ontario

1.1 Deer biology

White-tailed deer (*Odocoileus virginianus*) range throughout North America, as far south as the Gulf of Mexico, and are at the northern-most edge of their distribution in Ontario. Prior to European settlement, white-tailed deer were mainly restricted in Canada to the northern shore of Lake Ontario and the St. Lawrence (Smith and Verkruysse, 1983). Expansion of mining, logging and railroads cleared mature forests in the north, and the resulting successional forests, forest edges and clearings provided new deer habitat and forage, allowing a northward migration of deer populations (Smith and Verkruysse, 1983). Presently they range from southern Ontario to the northern shore of Lake Huron, with populations along the northern shore of Lake Superior near Thunder Bay and in the Lake of the Woods and Kenora areas (Appendix 1.).

While deer are mainly a forest or forest edge species and spend little time in large open areas, they require a mixture of forest and open areas and thrive in disturbed, successional areas (Voigt et al. 1992). During the summer months, deer range over large areas of mostly secondary forest gathering browse, consisting mainly of high protein and energy foods such as growing tips or shoots, for body development, antler growth and lactation (Verme and Ulrey 1984). In the fall, deer switch to high carbohydrate food sources such as clover, acorns or other "mast" crops, to accumulate fat stores for the winter (Verme and Ulrey 1984). In order to deal with the cold, deep snow winters in northern climates, deer have adapted their behaviour to reduce energy loss. In areas with high snowfall, deer migrate to traditional winter areas called "yards"

(Broadfoot et al. 1996), which are generally areas of high conifer abundance, predominately eastern hemlock (*Tsuga canadensis*) and eastern white cedar (*Thuja occidentalis.*) (Bellhouse 1993). The dense forests intercept snowfall to facilitate movement and access to winter food (Verme 1966, Ozaga 1968), while also providing shelter from wind and cold minimizing heat loss (Moen 1976). Yarding behaviour also produces trails in snow, thereby reducing energy expended during foraging and possibly aiding in escaping predators (Nelson and Mech 1991), though the anti-predator effects of yarding have been questioned (Poszig and Theberge 2000). Other physical adaptations for surviving winter include lower activity and reduced metabolism to conserve energy (Moen 1976). Deer browse in the winter is generally low quality, high fiber food such as conifer leaves, arboreal lichens and woody shrubs, and does not meet their energy requirements (Voigt et al. 1992). Therefore, deer are required to use their accumulated fat stores for additional energy.

Winter habitat is generally only 10-15% the size of summer habitat (Broadfoot et al., 1996). Since winter habitat is much smaller, deer tend to be at a higher % of carrying capacity (i.e. maximum population that can be supported) during the winter (Kw), than during the summer (Ks). As a result, Kw is limiting, and deer populations do not generally reach high percentages of Ks (Voigt et al., 1992).

Deer breed during the fall from early November to December. Adult does breed first, followed by yearling does in late-November and fawns in early December (Voigt et al. 1992), as fawns and yearling must obtain sufficient body size to breed (Ozaga and Verme 1982). Forage quality, weather conditions and population size in the summer all play a role in the number of deer that breed and the number of offspring produced

(Verme and Ullrey 1984). Does that are not bred until late in the season will have late born fawns with reduced chance of survival (Ozaga and Verme, 1982). The number of embryos per deer also depends on deer physical condition and may be lower at high population densities (McCullough 1979, Severinghaus and Moen, 1983).
Females over-winter pregnant and therefore have high energy demands. Harsh or long winters reduce pregnant doe fitness and may lead to abortion of fetuses or underweight and malnourished fawns at birth in the spring, many of which die within days of birth (Verme 1977). The post-natal loss of fawns may have a greater effect on population than direct winter mortality of deer (Verme 1977). The trade-off however is that does that lose fawns in the spring may be in better condition to breed the following fall for not having to nurse all summer (Voigt et al. 1992).

Sources of non-hunting mortality include predation (wolves, coyotes, black bear), illness, motor vehicle collisions and illegal poaching. Direct summer mortality of deer in Ontario is thought to be low for adults, about 3-7% of the annual mortality based on radio-tracking experiments (Voigt et al. 1992). Fawn mortality may be higher but rates are not known due to the difficulty in locating and tracking fawns. Winter mortality, mainly due to starvation and predation, is likely greater than summer, though the largest effect of winter may be the post-natal death of fawns.

1.2 Harvest Management

Regulations to manage deer harvests in Ontario have existed since the early 1800s. From 1918 to 1979, the main regulatory instrument was the length of the deer-hunting season. During this period, hunters were required to obtain licences and were limited both in the period during which they could hunt and their total kill, but were generally not regulated with respect to either where they hunted or the sex or age of deer killed.

Strong regulations on deer harvest were first introduced in the late 1970's, and are currently managed by the Ontario Ministry of Natural Resources (OMNR) following regulations set out in the Fish and Wildlife Conservation Act, 1997 (which replaced the previous Game and Fish Act in 1998). Following low annual harvests in the late 1970s and a (presumed) decline in the provincial deer population, a selective harvest system was introduced in 1980 and remains in place today. The selective harvest system places limits on the number of does or fawns (antlerless deer) that may be killed. All hunters are restricted to a maximum of one deer, and only those issued selective harvest permits (called tags) may take antlerless deer.

For the purposes of wildlife management (including deer), Ontario is partitioned into a number of Wildlife Management Units (WMU). Annual tag allocations are set by WMU and are issued through a lottery, with each tag being valid only in the WMU from which it was issued. The number of hunters taking only bucks is in general not controlled, though there are "controlled hunt" WMUs, where the total number of hunters is regulated. Controlled hunts are used mainly in the southern parts of the province, where reduced forest cover limits hunting opportunities and a large proportion of the forested lands are privately owned. Where controlled hunts exist, they are generally implemented to try and ensure a modicum of hunter safety. Areas with a controlled harvest may still also employ a selective harvest for management purposes. .

While all legal deer harvest takes place in the fall, the duration and timing of the deer season varies across WMUs. Indigenous people can hunt all year for their own personal and community consumption in areas they have traditionally hunted or that are covered by treaty. Most WMUs run an open firearm season (rifle, shotgun, or muzzle loading) for two weeks, with longer archery-only seasons before and/or after the firearm season. Seasons may also have restrictions on whether or not non-Ontario residents are allowed. Landowners may apply for permits to remove nuisance deer from their property, but only during regulated hunting seasons.

1.3 Deer Management Areas

Most deer management and reporting takes place at the WMU level. WMUs are grouped together in eight Deer Management Areas (DMAs), originally derived from a combination of biophysical, climatic, deer habitat and deer population parameters (Voigt et al., 1992). The boundaries were subsequently modified to correspond to newly developed federal ecoregion classifications (Wickware and Rubec, 1989) and to WMU boundaries. Details of the eight Ontario DMAs are given in Appendix 1.

2. Data Sources

2.1 Deer harvest

2.1.1 Provincial Mail Survey

There are no direct, systematic measures of harvest in any Ontario WMU. Rather, harvest estimates are derived from a Provincial Mail Survey (PMS) sent each year to a pseudo-randomly selected (every *x*th licence) subset of deer licence holders. Historically, fewer than 10% of licence holders were surveyed annually and this percentage has declined in recent years. In the survey, hunters are asked whether or not they hunted, and if so, in which WMU they hunted most. They also report the number of days spent hunting, the age (fawn versus adult) and sex of any harvested deer, and the number of deer seen. The PMS does not ask respondents to report on the method of hunting (e.g. bow versus gun, party versus individual), whether the respondent had an antlerless tag, or the type of season (firearm versus bow only).

With the exception of the number of survey respondents, all data in the electronic PMS database maintained by the Ontario Ministry of Natural Resources (available from Wildlife Section, Fish and Wildlife Branch, OMNR) are extrapolations based on the raw survey data; the raw data themselves are not retained in electronic form. Extrapolated estimates are based on the total number of license holders for the province (X), records of which are maintained by the OMNR. Extrapolated values were derived by dividing X by the total number of survey respondents (including both those who hunted and those who didn't) (Y) to obtain an extrapolation factor (γ).

$$\gamma = X / Y \qquad (1.1)$$

Surveys are assigned to the WMU in which the respondent indicated they hunted most. Respondents who did not hunt are not assigned to any WMU and are only used in the calculation of γ. The reported number of hunters (H), days hunted (E), deer seen (S) and killed (K) are multiplied by the extrapolation factor to obtain the extrapolated totals for each WMU (x) and year (t):

$$\hat{H}(x,t) = H(x,t) \cdot \gamma \qquad (1.2)$$

$$\hat{E}(x,t) = E(x,t) \cdot \gamma \qquad (1.3)$$

$$\hat{S}(x,t) = S(x,t) \cdot \lambda \qquad (1.4)$$

$$\hat{K}(x,t) = K(x,t) \cdot \gamma \qquad (1.5)$$

The PMS was discontinued in 1999 and has yet to be replaced.

2.1.2 Post Card Survey

Estimates of antlerless kill may also be obtained from the provincial Post Card Survey (PCS), begun in 1987, which is sent only to tag holders. Return rates (over 90% in some WMUs in some years, (mean = 45 ± 25%) for the PCS are considerably greater than for the PMS; hence, extrapolation factors for the PCS are considerably smaller. But because only tag-holders are surveyed in the PCS, it cannot be used to estimate the total number of hunters or the total buck kill. The PCS asks tag-holders to indicate their hunting effort and the sex and age of any deer killed. Some years also include deer seen, but those records are sparse and unsystematic. For a few WMUs and years, reported effort and kill were extrapolated to all tag holders and apparently the reported raw data were not retained.

2.1.3 Big Game Mortality Files

The Big Game Mortality Files (BGM) are maintained by the OMNR and include records of dead deer observed by OMNR staff. Most of these data come from Big Game Harvest Cards (BGHC) completed by OMNR staff at check stations set up at hunt camps or on roads out of popular hunting areas in order to interview hunters and take biological measures of deer killed. Some data come from deer parts (antlers, teeth, etc) turned in later or measurements reported by individual hunters to OMNR staff. There is nothing in the records to indicate who completed the card. Other data in the file are from export permits for non-resident hunters and records of non-hunting mortality gathered from a variety of sources such as dead deer surveys, reported vehicle collisions, etc. The availability of non-hunt mortality data varies substantially over years and between WMUs, as does the effort expended to obtain it.

Records in the BGM indicate the date and location of mortality (WMU and often township and/or UTM grid location) and the cause of death. Deer are aged (by tooth wear or incisor sectioning) and sexed. Several physical attributes may have been reported, but not all records contain all measurements. These measurements include weight, antler beam diameter, and antler points. For females, the number of fetuses may be recorded, as may whether they were lactating. OMNR staff takes the majority of all physical measurements, with the possible exception of antler beam diameter and antler points.

2.2 Weather data

2.2.1 Environment Canada Weather Data

Weather data were obtained from the Canadian Daily Climate; Eastern Canada 1998 CD-ROM published by the Climate Products and Publishing Division, Climate and Water Systems Branch, Environment Canada. The CD contains daily temperature, precipitation and snow on the ground for over 3000 stations in eastern Canada from as far back as the early 1900's to 1998 taken from the Environment Canada Archives. Minimum and maximum temperature, measured 1.5 m above the ground, are recorded for each 24-hour period, starting at 0600 Greenwich Mean Time, and are used to calculate the daily average temperature. Rain, freezing rain, drizzle and hail are measured in a standard, cylindrical Canadian rain gauge (40cm high with 11.3-cm diameter), 2 to 4 times per day. Snowfall on the ground is measured at several points using a snow ruler and then averaged. Total precipitation is the water equivalent of all types, with snowfall being converted by either dividing the measured values by 10 or more accurately at principal stations by melting snow collected in a Nipher gauge, set to prevent blowing snow from entering.

2.2.2 Snow Network for Ontario Wildlife

Since 1952, Ontario has operated the Snow Network for Ontario Wildlife (SNOW) designed primarily to generate data on winter conditions for deer management. The original 192 snow courses across the province were reduced to 100 in 1989, 68 by 1994 and 55 in 1996. Snow courses were designed to represent snow conditions in each WMU in the province. For each course, 10 stations are measured for snow depth and sinking depth. Winter chill (a combination of temperature and wind) was also measured at some stations. In all, snow depth (cm), snow crust (given a letter code), snow penetration gauge, chillometer readings (kWh) and observations of deer mobility and mortality are recorded at each individual snow course. These data are used to compute a variety of winter severity indices including the Passmore Snow Severity Index (PSSI), based on snow depth and crust type, and the Ontario Winter Severity Index (OWSI), based on snow depth, snow penetration and winter chill. Snow depth index (SDI), the cumulative total of weekly average snow depth, is the most simple to calculate and widely available measure of winter severity. Winter severity, based on SDI, is classified as mild (<590 cm), moderate (591-760) and severe (> 760) (Warren et al., 1998). Previous analysis by the OMNR has shown correlation between PSSI, OWSI and SDI, though actual correlation values were not provided by the authors (Warren et al., 1998). The OMNR use winter severity values to predict winter adult and fawn mortality and the availability of forage for use in population management and to determine if emergency winter-feeding is required.

2.3 Landcover Data

National Scale Ontario Land Cover maps were used to calculate land cover and patch metrics in ArcView 3.2. These 1:250,000 scale maps, available free through the geogratis website (www.geogratis.gc.ca) are a lower resolution version of the Provincial Scale Land Cover maps. There are 15 classes of land cover, with a minimum feature area of 50 ha and a pixel size of 100 m. The maps were created between 1986 and 1997 with most completed in the early 1990s. Updates to forest cover classification due to burns and cutting were added in 1996 for most coverages.

3. Variables and Measures

3.1 Harvest Variables

For each WMU (x) and harvest year (t), defined as the calendar year in which the fall harvest occurred, estimated values were taken from the PMS:

$R(x,t)$ ≡ total number of survey respondents that hunted

$\widehat{D}(x,t)$ ≡ total adult (≥1 year) doe kill

$\widehat{B}(x,t)$ ≡ total adult (1+ years old) buck kill

$\widehat{F}(x,t) \equiv$ total fawn (<1 year old, male or female) kill

$\widehat{A}(x,t) \equiv$ total antlerless kill = $\widehat{D}(x,t)+\widehat{F}(x,t))$

$\widehat{K}(x,t) \equiv$ total kill = $\widehat{D}(x,t)+\widehat{F}(x,t)+\widehat{B}(x,t)$

$\widehat{H}(x,t) \equiv$ total number of hunters

$\widehat{E}(x,t) \equiv$ total number of days hunted by all hunters

$\widehat{S}(x,t) \equiv$ total deer seen by all hunters

PMS data were available for all WMUs in the Algonquin Highlands from 1977-1997. The actual number of antlerless permits (or tags) issued (*P(x,t)*) was obtained from the Ontario Deer CD-ROM. As noted above, with the exception of *R(x,t)* and *P(x,t)*, all variables are extrapolations. For some WMUs and years, the number of returned surveys might be quite small (as few as a single survey); the data are extrapolated 5 - 20-fold and are of unknown and questionable accuracy.

3.2 Productivity

Surrogate measures of productivity rates were obtained from the Big Game Mortality Files (BGM). Two potential measures of reproductive rates were recorded at OMNR check stations: the average number of embryos per doe ($\overline{ED}$) and the proportion of does lactating (*LD*). The Fawn: Doe ratio (*FD*), which may provide a rough measure of fawn recruitment into the fall hunt and incorporates both birth rate and fawn survival can be estimated both from the PMS and the BGM. Hunter-reported FD from the PMS is often presumed to be biased by hunters classifying fawns as does. The accuracy of these data and their relationship to actual productivity or recruitment are unknown.

3.3 Physical Condition

Measures of yearling buck (1-year-old deer) physical condition are often used as indicators of population size in relation to the quality of summer habitat (i.e. how close is the population to summer carrying capacity) and have been shown to relate to measures of productivity (Severinghaus and Moen, 1983). Males use the summer feeding period for antler and body development leading up to the fall breeding period. Yearling buck condition in the fall harvest should be an indicator of the quality and quantity of available forage during the preceding summer, while condition of bucks > 1 year old will reflect both summer forage and the cumulative effects of preceding seasons. In our analyses, the average male yearling antler beam diameter ($\overline{Y}$) and body weight ($\overline{W}$) were used as measures of physical condition.

3.4 Weather Variables

Weather data for a particular WMU were obtained from the Environment Canada weather station closest to the geographical center of the WMU. Because weather data were not necessarily recorded at all stations in all years, it was sometimes necessary to use different stations for a single WMU. Weather data for each harvest year (t) were calculated for the winter, spring and summer periods between harvests t and t+1. For example, 1989 weather data spanned the time period following the 1989 November hunt, i.e. winter (Nov. 1989 – March 1990); spring (Apr. 1990 – May 1990); and summer (June 1990 – August 1990). Daily total precipitation and average temperature data were used to calculate the following variables for each WMU (x) and year (t);

$R_P(x,t) \equiv$ total rainfall from April to May (spring)

$R_S(x,t)$ ≡ total rainfall from June to August (summer)

$R_W(x,t)$ ≡ total snowfall from November to March (winter)

$T_P(x,t)$ ≡ average daily temperature, April – May (spring)

$T_S(x,t)$ ≡ average daily temperature, June – August (summer)

$T_W(x,t)$ ≡ average daily temperature, November – March (winter)

The Snow Network for Ontario Wildlife (SNOW) provided another measure of winter severity (Ws), the snow depth index (SDI) calculated as the cumulative snow depth for the entire winter (cm). For each WMU (x) and harvest year (t), $Ws(x,t)$ was calculated from SNOW courses, based on formulae provided by the OMNR (Warren et al., 1998). Due to changes in sampling, not all courses used in the formulas were available for all years. In cases of missing data, values were taken from the nearest snow course with data, with the result that the particular courses used for an individual WMU may have changed over time, and often the same course was used for multiple WMUs.

3.5 Hunt Conditions

The legal deer season varied between WMU and years and includes both firearm and archery only seasons. The start and end dates of the total deer season (firearm and archery combined) were taken from paper records provided by the OMNR. Records were only available from 1983 onwards. Daily weather data during the hunt season from the Canadian Daily Climate Data were used to calculate the number of days with snow (DS), the number of days with rain (DR), the number of days below zero (DB), the average snow depth in cm ($\overline{CS}$), average rainfall in cm ($\overline{CR}$) and temperature in °C ($\overline{CT}$).

3.6 Habitat Variables

The Ontario Land cover maps in decimal degrees were projected to match a digital WMU/DMA map provided by the OMNR. The map was projected to a Lambert Conformal Conic, with a central meridian of –85 latitude, a projection origin of 00 00 00, standard parallels of 44 30 00 and 53 30 00, a false easting of 930,000 and a false northing of 6,430,000. The two projected maps were overlaid and the land cover map was clipped using the WMU theme, producing a landscape for each WMU. During digitizing by the map's creators, many relatively loosely connected patches were classified as one polygon, creating large, jagged patches that spanned multiple WMU. Any trans-boundary patches were cut at the WMU border, creating artificial edges and underestimating the size of patches at the border. However, this was necessary to prevent the large portions of patches outside of the WMU contributing to forest cover calculations of the WMU in question. Some of the original digitized OLC grids did not match up perfectly and as a result forest patches that span two grids are sometimes classified as two patches instead of one, producing an underestimate of mean patch size in areas with large forest patches.

For each WMU landscape, Patch Analyst (3.2) extension for ArcView was used to calculate the total area (km^2) of forest (L_F), agricultural land (L_A), urban/developed land (L_U) and the total land area (excluding water) (L_T).

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Chapter 2: Deriving an index of white-tailed deer population density from harvest data.

Introduction

For managed wildlife species, virtually all management interventions are based – at least in part – on (real or imagined) changes in population size. Our main objective in this study is to identify the factors that regulate white-tailed deer population dynamics, and specifically those that have some potential to be managed. As such, we require some measure of population density and/or population size. Because direct estimates of population size or density are difficult to obtain, we are usually forced to rely on indirect measures derived from the harvest itself.

Catch per unit effort (CPUE) obtained by dividing some index of catch by some measure of effort, has long been used to estimate either population size or population density (Leslie, 1939, Ricker 1958, Caughley 1977, Bishir and Lancia, 1996). For deer, two measures of catch are often available: the number of deer seen by hunters, and the number of deer harvested. Previous research suggests that, at least in some circumstances, CPUE based on deer seen and deer harvested are closely correlated and, moreover, are correlated with other (independent) estimates of population size or density (i.e. cohort analysis, spotlight counts, etc.) (Roseberry and Woolf 1991; Fryxell et al. 1991)

In order for some CPUE ($Y= C/E$) measure to be an unbiased measure of deer population size or density, (a) "catch" (i.e. kill or deer seen) must be linearly related to effort (using the quotient of C by E assumes a linear relationship) and (b) Y must be linearly related to the true population size or density (Rosebery and Woolf, 1991). The validity of the first assumption can be assessed directly for both deer seen and deer harvested as we have measures of effort for both. The second assumption cannot be tested without an independent measure of population size or density. Due to the difficulty and cost in obtaining direct estimates of population size (i.e. spotlight counts, aerial surveys) there are no such data available for Ontario. Pellet count surveys have been carried out sporadically in some areas, though often for geographic areas that compose only part of a WMU (e.g. Canonto deer yard) and are not generally applicable to this study. In addition, pellet counts, as an estimate of population density, are of questionable accuracy (Fuller 1991).

However, if Y is unbiased, the conditional probability of a deer being "caught", given a certain population size/density, must be independent of any factor that changes with population size. For CPUE based on harvest, the probability of a deer being harvested will be the product of the probability of encountering a deer (i.e. encounter rate) and the probability of successfully killing any deer encountered (i.e. hunter efficiency). By contrast, a CPUE based on deer seen depends only on the former probability.

The encounter rate will be affected by any factor that increases deer-hunter interactions (e.g. hunter numbers), forces deer to congregate in smaller areas during the hunt (e.g. snow during the hunt), or affects deer visibility (e.g. habitat or weather conditions). Population estimates based on CPUE also assume that all deer are equally visible irrespective of age and sex. Differences in sex and/or age ratios for hunting versus non-hunting mortality have been demonstrated, but it is not clear whether the difference was due to visibility of deer or hunter selectivity (Rosebery and Klimstra, 1974; Coe et al., 1980). In any event, unequal visibility will not bias the index unless visibility or population age-sex structure is related to population size. Hunter success is also related to a variety of largely intangible factors such as hunter skill, experience, and equipment. As long as these factors are independent of population size (e.g. average hunter skill does not increase with population), these factors should not bias population estimates derived from CPUE.

In a selective harvest system, tag status may affect hunter success, as those without tags are restricted to only half the population (bucks only). Moreover, under such a system, the number of tags issued tends to respond to perceived changes in population size, thereby inducing a positive correlation between the two. If indeed such a relationship exists, and the number of tags issued affects hunter success, then CPUE based on the harvest will not be an unbiased estimate of population size. Hunter selectivity may also lead to biased population estimates based on harvest if selectivity depends on population size (for example, if at high population density hunters actively pass up one sex or age group over others).

Here we compare CPUE indices based on (a) deer seen and (b) deer harvested in an attempt to determine which is more likely to provide a less biased estimate of population size /density. To do so, we investigate their relationships with hunter effort, and the effects of tags, hunter density, and weather during the harvest on CPUE estimates based on deer seen and harvested. Further we assessed the consistency of both measures across geographic regions to determine their usefulness as a province wide index of population. Because we have no independent estimate of population size or density, such a comparison does not provide any information on the absolute reliability of either measure as an index of (true) population size.

Methods

Ontario is partitioned into Wildlife Management Units (WMU) for the purposes of harvest management and reporting. WMUs are in turn grouped into eight Deer Management Areas (DMA), whose geographical boundaries are based on physiographic and climatic features (see Chapter 1 for more details). The Algonquin Highlands (AH) DMA in central Ontario (Appendix I) is the most heavily hunted DMA in the province and has the most complete set of harvest records of any DMA in the province. A selective harvest has been in place for all WMUs in the AH since 1980, and the number of tags issued has changed significantly from 1980 to present. Due to its large number of surveyed hunters and the high quality of the harvest records, AH was selected for the main part of the analysis.

The relationships between reported deer seen ($S(x,t)$), deer harvested ($K(x,t)$) and effort ($E(x,t)$), measured as total reported days hunted, were explored using data reported (i.e. unextrapolated values) in the Provincial Mail Survey (PMS) (see Chapter 1 for further details on data sources) for all 15 WMU (x) in AH for 1980-1997.

For each WMU (x) and harvest year (t), hunter density (θ),the estimated total number of hunters ($\hat{H}(x,t)$) per km^2 of forest in the WMU ($L_F(x)$) was calculated as

$$\theta(x,t) = \hat{H}(x,t) / L_F(x) \qquad (2.1)$$

The number of tags issued (*P(x,t)*), taken from digital and paper records provided by OMNR staff, was used to calculate the estimated proportion of hunters with tags (ρ) for each WMU and year

$$\rho(x,t) = P(x,t) \,/\, \hat{H}(x,t)\,. \qquad (2.2)$$

Weather conditions during the hunt for each WMU and year were taken from Canadian Daily Climate, Eastern Canada 1998 CD-ROM (see Chapter 1 for further details). These data include number of days with snow (*DS*), average snow depth ($\overline{CS}$), days with rain (*DR*), average rainfall ($\overline{CR}$), and the number of days below 0 °C (*DB*) and average temperature ($\overline{CT}$).

We first explored the relationship between catch and effort by fitting Type I regression models with S(x,t) or K(x,t) as the dependent variable and E(x,t) as the independent variable. We then investigated the possible effects of weather conditions during the hunt, ρ(x,t) and θ(x,t) by evaluating the contribution of these variables to overall model fit. Stepwise multiple regression was run forward and backward, with entry/removal alpha =0.15 to determine the best model for the AH data.

Relationships determined for AH were then investigated using data from the remaining 7 DMAs to determine the (geographic) generality of the models derived. To reduce sampling errors due to small survey samples, we included only WMUs and years for which at least 20 surveys were returned. Even with this restriction, the number of survey respondents in other DMAs, especially in the northern part of the province, were considerably lower than for the AH (Table 2.1).

Results

Algonquin Highlands

Reported log 10 deer seen was strongly positively ($r = 0.90$) correlated with log 10 total kill (Fig. 2.1). There was a strong linear relationship between log10 deer seen and log 10 hunter days ($b = 1.02 \pm 0.02$, $t = 54.13$, $df = 245$, $p < 0.001$, $R^2 = 0.92$, $RMS = 0.009$) (Fig. 2.2a), with a slope not significantly different from 1 ($t = 1.31$, $df = 245$, $p = 0.20$). Considerable variation among WMUs in the average number of deer seen resulted in a statistically significant, but small contribution to model fit by WMU ($F = 6.77$, $df = 13$, $p < 0.001$, $R^2 = 0.94$, $RMS = 0.007$). There was marginal evidence that the slope of the deer seen – effort relationship varied among WMUs ($F = 2.22$, $df = 13$, $p = 0.01$), but it contributed little to the overall model fit beyond that explained by effort and differences in WMU mean deer seen ($R^2 = 0.95$, $RMS = 0.007$).

Log 10 kill was also positively related to log 10 effort, but more weakly than was log 10 deer seen ($b = 1.11 \pm 0.04$, $t = 27.8$, $p < 0.001$, $R^2 = 0.76$, $RMS = 0.040$)(Fig. 2.2b). Moreover, the slope of this relationship was significantly different from 1.0 ($t = 2.95$, $df = 245$, $P = 0.004$). Differences in the average kill among WMU also resulted in a statistically significant WMU effect, ($F = 3.95$, $df = 3$, $p < 0.001$, $R^2 = 0.80$, $RMS = 0.035$). There was no evidence that the slope of the relationship between kill and effort varied among WMU ($F = 1.31$, $df = 13$, $p = 0.20$).

For deer seen, the effects of other factors, after accounting for effort, were small (Table 2.2a). Neither hunter density, the proportion of tag-holders or weather conditions during the hunt, alone or when combined, made significant contributions to model fit (Table 2.2a). Of all tested predictor variables, only average snowfall during the hunt had a statistically significant effect, though only a small contribution to model fit (Table 2.2a). By contrast, log 10 total kill was positively related to the proportion of tag-holders when effort was statistically controlled ($b = 0.514 \pm -0.037$, $t = 13.9$, $P<0.001$ (Fig. 2.3), resulting in a substantial improvement in model fit ($R^2 = 0.87$, $RMS=0.021$). After accounting for effort and the proportion of tag-holders, kill also showed statistically significant positive associations with hunter density and snow during the hunt, which made little contribution to overall model fit (Table 2.2b). However, after accounting for the effects of hunter density and tags on kill, the partial coefficient for effort ($b = 0.998 \pm 0.025$) was no longer significantly different from 1 ($t = -0.8$, $df=244$, $p = 0.42$).

Consistency across DMA

In order to be an effective province wide index of population, the expected catch for any level of effort should be consistent for all geographic areas. Linear regressions for both measures of catch (deer seen and killed) with effort were run for each DMA individually. We then compared the geographic consistency for deer seen and deer killed models by plotting the partial regression coefficients (b) versus the residual mean square (RMS) for each DMA. This allows us to assess the degree of similarity between DMA in both the form (vertical grouping) and strength (horizontal grouping) of the respective relationships (fig. 2.4). The individual DMA were more tightly grouped for deer seen than deer killed, in both the form and strength of their models. The deer seen – effort relationship was quite similar between DMA, with the exception of Thunder Bay (TB) which had a relatively poor model fit. Thunder Bay had the fewest data points (N=37) and the lowest mean number of surveys returned ($\overline{N} = 41$).

Reported log 10 deer seen for the other DMA pooled (excluding AH) was strongly related to reported hunter days ($N = 653$, $b = 0.886 \pm 0.022$, $t = 40.4$, $p < 0.001$, $R^2 = 0.71$, $RMS = 0.032$) (fig. 2.5), though unlike AH, the slope was significantly different from 1.0 ($t = -5.18$, $df = 652$, $p < 0.001$). There was a significant difference between DMA (including AH) in mean deer seen ($F = 30.1$, $df = 6$, $P < 0.001$) which when accounted for significantly improved model fit (without DMA: $R^2 = 0.72$, $RMS = 0.032$, with DMA: $R^2 = 0.82$, $RMS = 0.21$). There was a statistically significant difference between DMA in the slope of the deer seen-effort relationship (Effort *DMA: $F = 7.01$, $p < 0.001$), which added little to the model fit ($R^2 = 0.82$, $RMS = 0.021$).

Discussion

When other factors are statistically controlled, both deer seen and total kill increased linearly with effort in the Algonquin Highlands, thereby satisfying at least one necessary (but not sufficient) condition for either to be an unbiased index of population size or density. Using log values of both deer seen and effort removes any non-linearity and is also necessary to account for heterogeneity of variance in deer seen at low versus high levels of effort.

However, deer seen in AH is independent of the number of tags issued, whereas kill shows a strong positive relationship. This is perhaps not altogether surprising; low tag allocations will restrict antlerless, and therefore total, kill leading to lower than expected kill for the effort expended, presumably since hunters are forced to pass on antlerless deer and are in effect hunting only half the population. Indeed, at the highly restricted kill associated with very low number of tags issued, CPUE based on kill may bear little relationship to actual population size or density. On the other hand, because, for given effort, the probability of sighting a deer is not related to the number of tags issued, changes in CPUE based on deer seen are not biased by tags.

Kill per unit effort in the AH was also positively related to hunter density, though only weakly. Effort and hunter numbers were highly correlated, and controlling for hunter density resulted in a linear relationship between kill and effort. This suggests that the observed non-linearity in the raw kill- effort relationship arises from increased hunter efficiency at high hunter densities. It has been suggested that the probable relationship between hunter efficiency and density is non-monotonic (Foster et al., 1997): at low hunter densities, increased hunter numbers result in higher efficiency as more deer are being forced to move out of hiding, until a point is reached when hunter interference becomes a factor and success rates fall (Foster et al., 1997). However, if the detected effect of hunter density (controlling for effort) on kill was due to increased deer visibility, we would expect to see a similar relationship with deer seen. Yet no such relationship was detected, so increased deer movement leading to increased sightings is a poor explanation for the hunter density effect. Increased efficiency at higher densities may reflect more hunters in areas where hunting is better (i.e. more deer, better access to deer, less cover, etc.).

Both deer seen and kill showed a positive relationship to the average snow depth during the hunt. In Ontario as elsewhere, white-tailed deer congregate in smaller winter areas (called "yards") with reduced snow cover which are thought to aid in preventing energy loss (Moen, 1976) predator avoidance, movement and locating forage (Ozaga, 1968, Nelson and Mech 1991). Snowfall may trigger deer movement into yards during the harvest, thereby increasing (local) densities and making them easier for hunters to locate. This is commonly cited as the cause for high harvests in 1990 and 1991 (Bellhouse, 1993). Although we were unable to determine whether there is an interaction between the effect of snowfall and population density that would bias CPUE based on both deer seen and kill, snowfall accounted for little variation in deer seen beyond that accounted for by effort, suggesting that for deer seen, such biases are small, and possibly negligible.

Geographic consistency is another important factor in determining the applicability of a CPUE index. Differences in the mean deer seen (or killed) per effort, presumably indicating differences in mean deer densities, observed between WMU and DMA, do not affect its use as an index. However, variance in the form or strength of the deer seen (or killed) versus effort relationship between DMA, would mean that the ability to catch (see or kill) a deer may not be consistent for all geographic areas. This would preclude using the same CPUE index in a population model for the entire province, without accounting for location, as the expected number of deer caught for any given effort level would then be dependent on geographic location.

Deer seen showed a larger degree of consistency than kill in its relationship with effort, across DMA, both in the form (i.e. coefficient) and strength of the relationship. The differences between DMA in the coefficients for deer seen versus effort, while statistically significant, did not have a major contribution to model fit. There is no evidence that the ability to see a deer varies greatly across the province. Therefore, one model to calculate deer seen per unit effort (DSPUE) can be used to generate a population index for the entire province, with likely only a minor loss in its accuracy. The same DSPUE value should indicate the same deer density (assuming DSPUE has any relationship to density) regardless of geographic location. This may not necessarily be true for Thunder Bay DMA, which had a relatively different coefficient, but the quality of the data on which it was based is suspect due to small numbers of hunters surveyed.

Deer seen, controlling for effort, appears to be the better index of population density, in comparison to kill, as it is (a) not affected by the number of tags or hunter density which may potentially bias CPUE indices based on kill and (b) its relationship is more consistent among DMA. Additionally, since a deer must be seen to be killed it seems reasonable to assume that any index based on kill would include all the biases of a deer seen index, plus any biases related to a hunter's ability to kill a deer seen. Differences between hunters in ability may influence the number of deer killed, but do not seem to affect the number of deer seen (Holsworth 1973). Catch per unit effort indices of population based on kill are likely to be biased by both the proportion of hunters with tags and hunter density and therefore would be poor indicators of population. Presumably these biases would affect other indices based on kill such as hunter success and tag filling rate.

Log 10 deer seen is linearly related to log 10 effort, and the difference between the expected and actual number of deer seen, for any given effort, should be related to changes in population size. The relationship between deer seen and effort, both in slope and model fit, was relatively consistent across DMA, and therefore the same model for calculating DSPUE can be used across the province. Without independent measures of population we have no way of assessing the true relationship between this index and actual population. However, from the harvest data collected by the OMNR, deer seen, controlling for effort, is best population density index available.

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List of Tables

Table 2.1. Total number (N) of WMU and years for which the number of surveys returned was ≥ 20 for each Deer Management Area (DMA) and the mean number of surveys ($\bar{R}$) for all WMU and year (±standard deviation).

DMA	N	$\bar{R}$ (±sd)
Lake of Woods	53	95 (54)
Thunder Bay	37	41 (19)
Sudbury	38	64 (45)
Algonquin Highlands	247	216 (164)
Manitoulian	35	202 (188)
Eastern Midlands	120	156 (116)
Central Agricultural	256	72 (63)
Southern Agricultural	114	74 (39)

Table 2.2. Multiple linear regression models predicting (a) log 10 deer seen (S) and (b) log 10 total kill (K) from hunter effort (E), proportion of tag-holders (ρ), hunter density (θ) and snow during the harvest ($\overline{CS}$) for the Algonquin Highlands, 1980-1997.

Dependent	Effect	*b (±se)*	*t*	*p*	*Model R^2*	*Model RMS*
(a) $\text{Log}_{10} S$	Log_{10} E	1.034 ±0.025	42.07	<0.001	0.93	0.008
	ρ	-0.004 ±0.027	-0.15	0.88		
	θ	0.001 ±0.009	0.13	0.90		
	$\overline{CS}$	0.002 ±0.001	4.25	<0.001		
(b) $\text{Log}_{10} K$	Log_{10} E	0.998 ±0.035	28.07	<0.001	0.90	0.018
	ρ	0.442 ±0.039	11.48	<0.001		
	θ	0.061 ±0.013	4.56	<0.001		
	$\overline{CS}$	0.004 ±0.001	5.56	<0.001		

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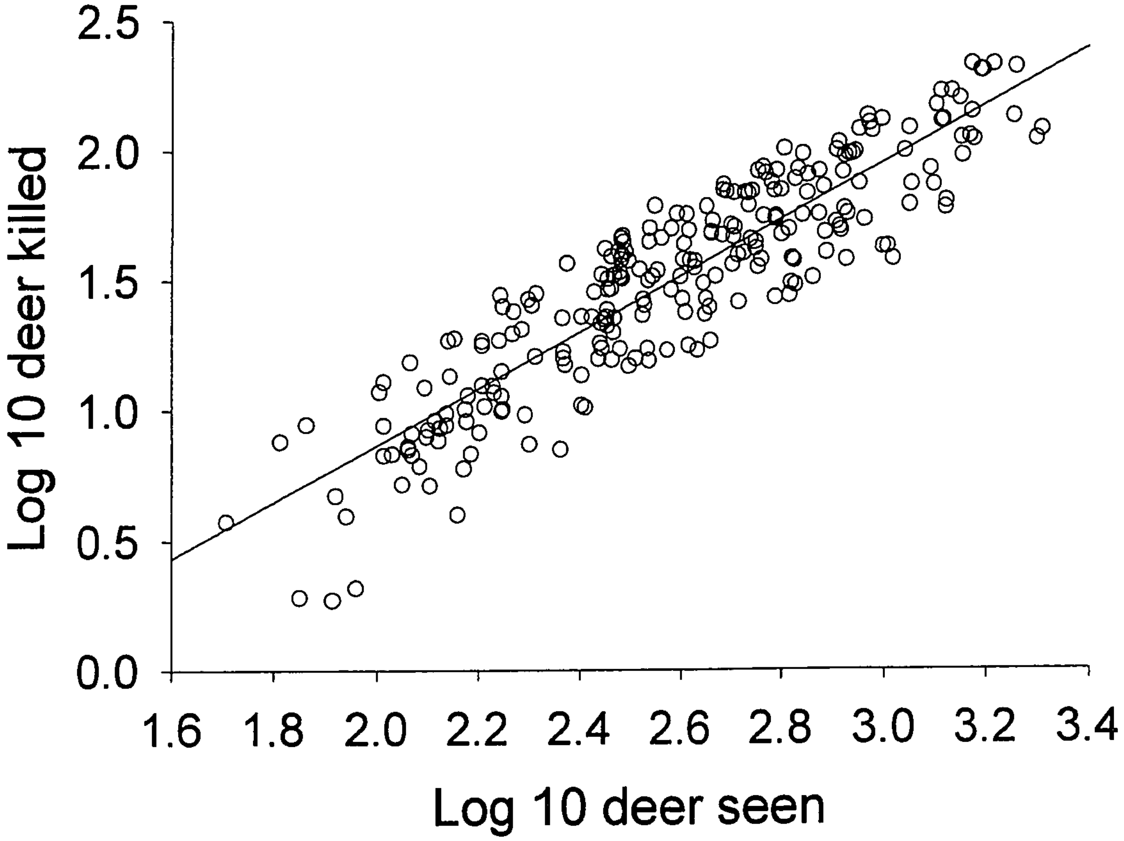

Figure 2.1. The relationship between the reported deer seen (log 10) and reported total kill (log 10) from the Provincial Mail Survey, for all WMU in the Algonquin Highlands DMA, 1980-1997.

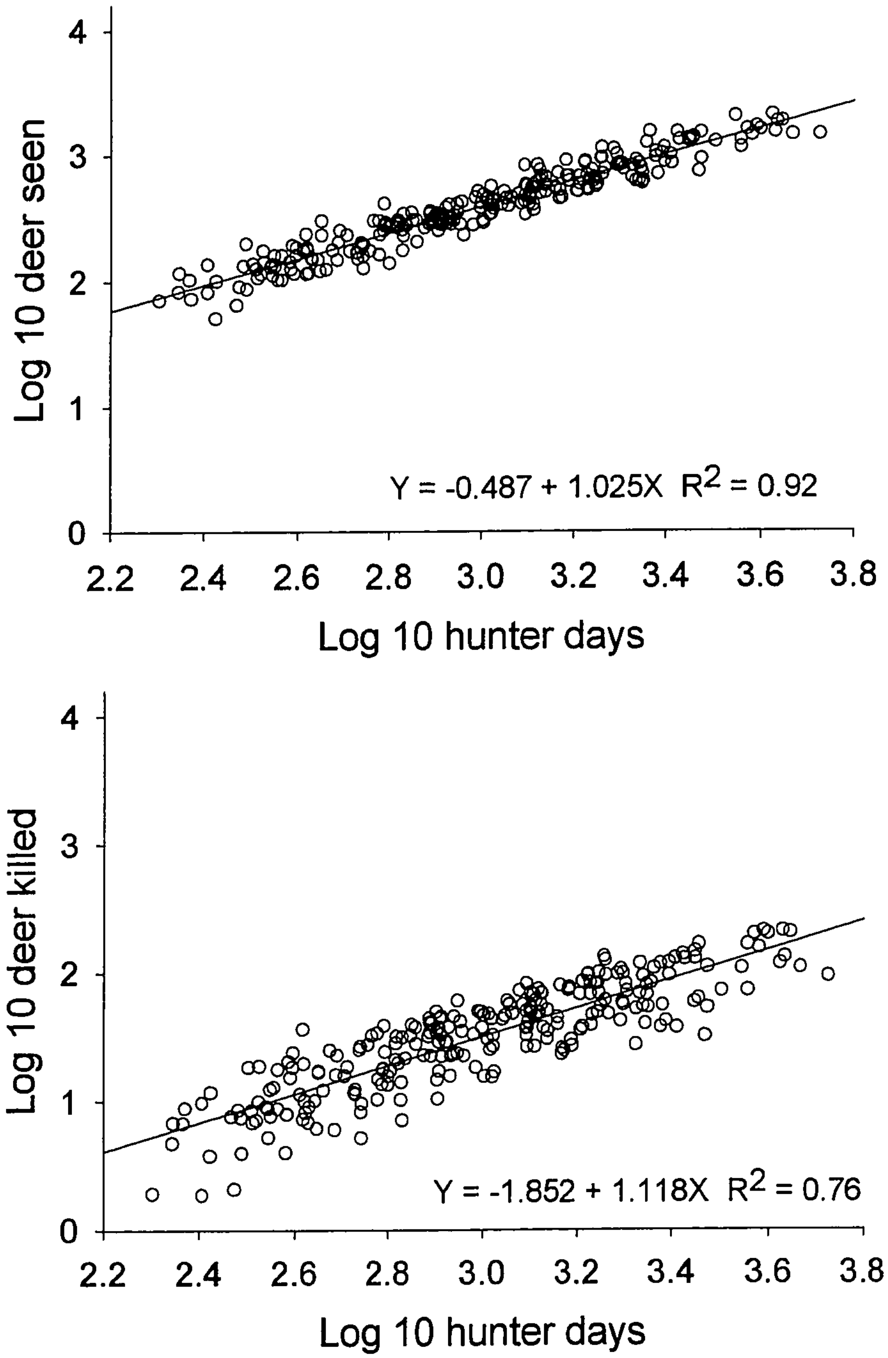

Figure 2.2. The relationship between the reported deer seen (log 10) (upper) and reported total kill (log 10) (lower) and reported hunting effort (log 10) from the Provincial Mail Survey, for all WMU in the Algonquin Highlands DMA, 1980-1997.

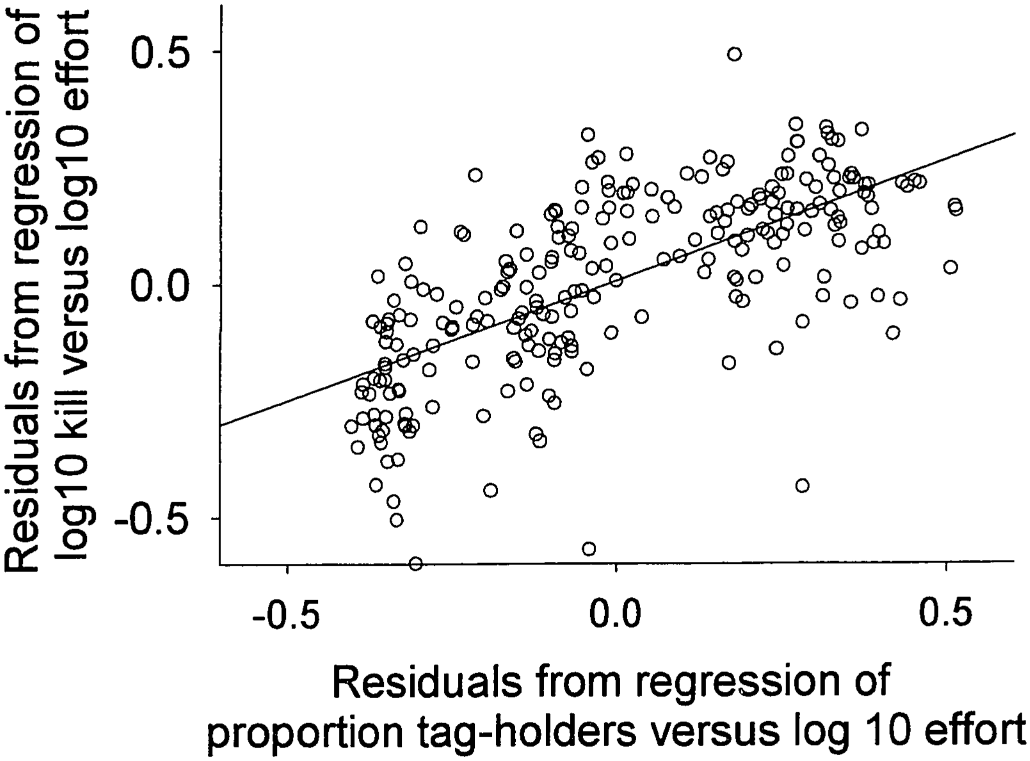

Figure 2.3. Full partial plot showing the relationship between log 10 kill and proportion of tag-holders, statistically controlling for hunter effort.

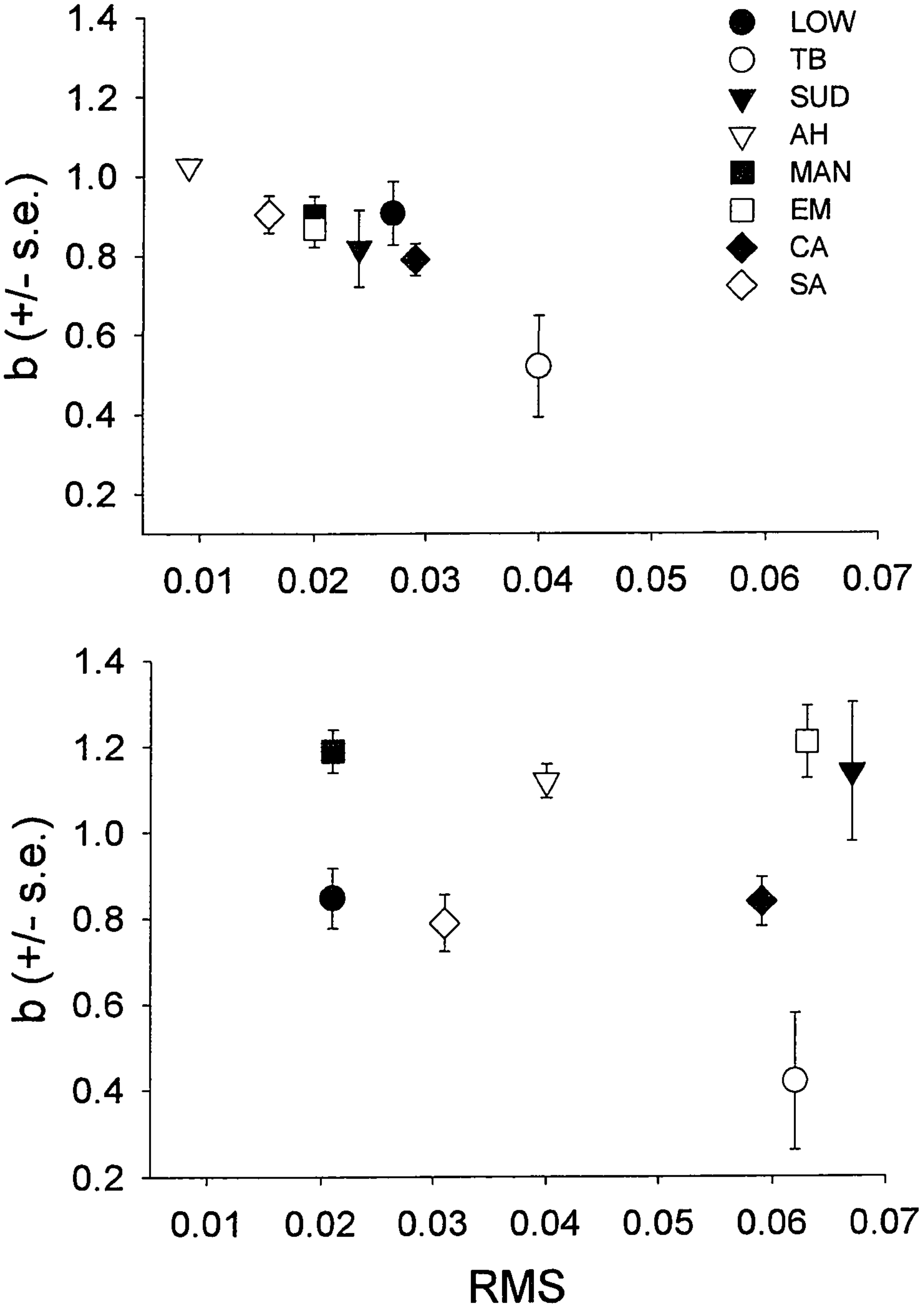

Figure 2.4. Partial regression coefficients (b) (± standard error) versus residual mean square (RMS) from linear regression of reported deer seen (log 10) (upper) and reported total kill (log 10) (lower) versus reported hunting effort (log 10) by DMA.

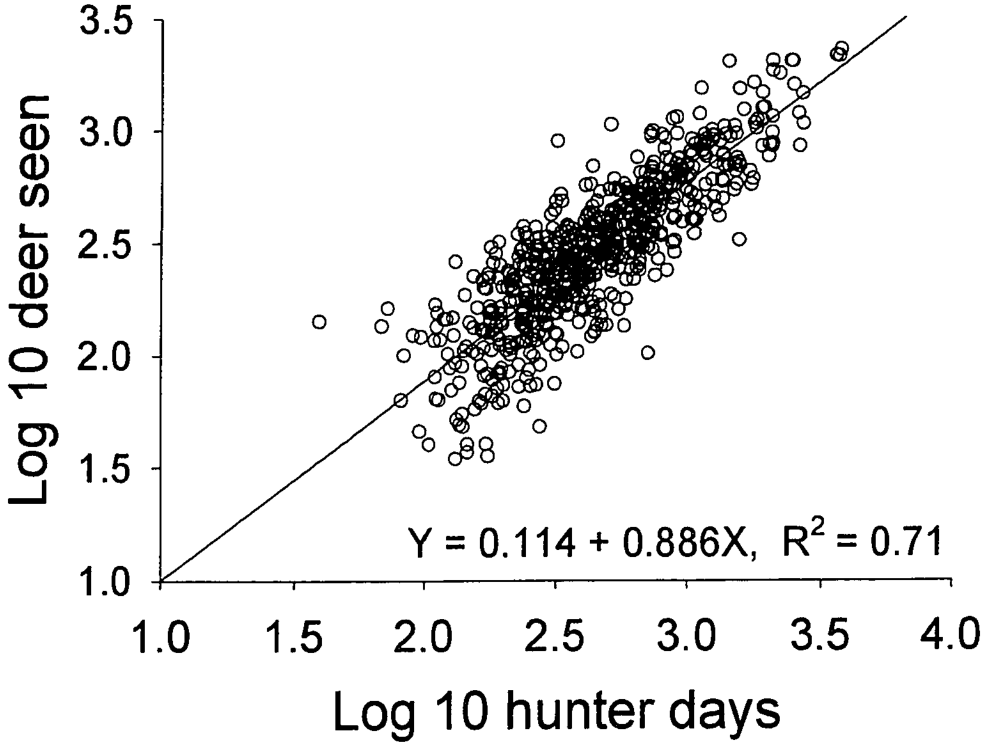

Figure 2.5. Reported deer seen (log 10) versus reported hunter effort (log 10) from the Provincial Mail Survey for WMU outside of the Algonquin Highlands DMA, for years with at least 20 hunters reporting, 1980-1997.

Chapter 3: The effectiveness of a selective harvest system in regulating deer kill in Ontario

Introduction

The goal of white-tailed deer (*Odocoileus virginianus*) management is to maintain populations at levels below where they are a nuisance, but sufficiently large so as to provide ample recreational hunting and viewing opportunities. Historically, in Ontario at least, a regulated sport harvest has been the main (and often only) tool available for managing deer populations. Indeed, wildlife management agencies across North America commonly use recreational hunts as inexpensive management tools, though surveys indicate that hunters do not see themselves in this role (Decker and Connelly, 1990).

As with most harvested populations, the guiding principle for deer management in Ontario, and throughout North America, has been the age-old concept of maximum sustainable yield (MSY) (Ricker, 1954). For species with density-dependent growth rates, the highest sustained yield (i.e. kill) can be achieved by maintaining the population, through harvesting, at the level where growth rate (recruitment) is maximal. A strategy for deer, as with most harvested populations, that is very difficult to apply in practice (Ludwig et al. 1993), due to the difficulties in obtaining accurate data and the natural stochasticity of the environment and deer demographic rates.

Prior to 1979, deer in Ontario were managed through one deer per hunter bag limits and the control of hunting season length, a management program that was relatively unsuccessful (Voigt et al. 1992). In 1980, the Ontario Ministry of Natural Resources (OMNR), in response to perceived low deer numbers in the late 1970s attributed to over-harvest and harsh winters, followed the lead of other North American management agencies and instituted a selective harvest system requiring hunters to have a permit (tag) to kill a deer without antlers (adult females or fawns of either sex) in most areas (Voigt et al. 1992).

After observing an apparent correlation between declining total harvests and increasing percentage of does in the harvest, Hayes and Gwynn (1977) first proposed that over-harvesting could be prevented by limiting the female harvest to some percentage of the buck harvest. Since, they argued, buck harvest is naturally limited at low levels by deer wariness and the inability of hunters to locate them, if female harvest was limited to some percentage of buck harvest, then there was little danger of over-harvesting. This system, should be effective in limiting kill, requires limited data collection and has the bonus of being philosophically agreeable to most sportsman (McCullough 1984).

This sex-linked strategy has been criticized for not being protective against over-exploitation, as it considered only the harvest ratio and not the proportion of the population removed (Downing 1980). However, other studies maintain a linked sex harvest strategy (LSHS), can be used efficiently to determine yields, safe from over-harvesting, simply from sex ratios in the harvest, without requiring data estimates of population size, carrying capacity or demographic data (McCullough et al. 1990, Lubow et al. 1996). Others have proposed similar systems that require some estimate of population size as a safeguard (Lancia et al. 1988).

Additionally, since deer are polygynous (i.e. one male can impregnate more than one female), theory predicts that population dynamics are driven primarily by mortality and reproductive rates in females. Moreover, in deer, there is empirical evidence to suggest that productivity and recruitment have stronger density-dependent relationships with the size of the female population (McCullough 1984, Teer1984) than with total population size. It has been suggested that deer populations can support very large buck harvests (as large as 80% of the buck population), as long as female harvest is limited (Dickinson, 1982).

Therefore, the assumption behind the selective harvest is that by regulating female kill (in practice antlerless kill as it is difficult in the field to differentiate fawns from does or between male and female fawns), managers would be able to best regulate population growth and maximize harvest yield. A low kill would allow populations to recover, and later increased doe kill would maintain desirable population levels to allow for maximum recruitment of fawns. As such, the system does not of itself regulate hunter numbers or buck kill.

The selective harvest is still in force throughout most areas in the province, though population levels have generally increased in most areas. Tags are issued by lottery for specific geographic areas, called Wildlife Management Units (WMU). While tags are assigned to individual hunters, "party hunting" in which a non-tag holder can transfer an antlerless kill to a member of their party with a tag, has been permitted since 1992, although there is little doubt that it commonly occurred previously (Bellhouse 1993).

Despite their widespread use, there have been few empirical studies of the effectiveness of selective harvest systems to regulate antlerless harvests or deer populations to the required (or expected) precision. Brown et al. (2000) advised wildlife management agencies to review their deer harvest control systems with respect to (among other criteria) (1) the ability of the agency to regulate the control mechanism (i.e. tags), (2) the reliability and precision of the control mechanism to regulate harvest and (3) the ability of the control mechanism to produce the desired end result (i.e. regulate population).

While OMNR has relatively tight control over the number of tags issued (criterion 1), it must be determined if tags are reliable as regulators of antlerless kill (criterion 2) and if antlerless kill indeed regulates population (criterion 3). We began by assessing criterion 2, by reviewing historical harvest data to determine the strength and shape of the relationship between antlerless kill and tags issued, deer population density and the number of hunters. The assessment of criterion 3 is presented later (Ch. 4).

We also looked at the relationship between kill per hunter, tags, hunter density and deer encounter rates to determine if other limits on kill existed which may affect the effectiveness of tags. The selective harvest is based on the assumption that the number of antlerless deer killed is related to the number of tags issued. In any hunt the total antlerless kill will be a function of the number of antlerless hunters and their success rate (kill per hunter) in getting an antlerless deer. Hunter success in turn is the product of the conditional probability of encountering a deer and the probability of killing a deer when encountered (i.e. hunter efficiency). Under the selective system, tags are used to set the maximum antlerless kill, with deviations from the maximum kill being related to the encounter rate and hunter efficiency.

If hunter success is limited by deer encounter rates, then you would expect a positive relationship between deer seen per hunter and the kill per hunter. We also looked for evidence that hunter interference may be limiting hunter efficiency. This hypothesis would predict a negative relationship between hunter density and hunter success, though the shape of this relationship may not be linear. The study was primarily conducted using data from the Algonquin Highlands (AH) Deer Management Area (DMA) in North-Central Ontario from 1980-1997. Results from AH were then tested in the other DMA to determine their scale of applicability.

Methods

Study Area

Ontario is partitioned into Wildlife Management Units (WMU) for the purposes of harvest management and reporting. WMUs are in turn grouped into eight Deer Management Areas (DMA), whose geographical boundaries are based on physiographic and climatic features (see Ch. 1 for more details). The Algonquin Highlands (AH) DMA in central Ontario (Appendix I) is the most heavily hunted DMA in the province and has the most complete set of harvest records of any DMA in the province.

Data for the other DMA were of lesser quality and quantity than in the AH. The number of returned surveys per WMU, due to lower hunting levels, is lower especially in the northern DMA (TB, SUD) and hunting seasons varied between WMU and years. Therefore the sample size (number of WMU and years) for the other DMA are lower than in the Algonquin Highlands and there is less continuity in the years studied. Due to its large number of surveyed hunters and the high quality of the harvest records, AH was selected for the main part of the analysis.

Following low harvests in the late 1970s and a presumed declining deer population, a selective harvest system was introduced in 1980 - and remains in place today - in all DMAs except the Southern Agriculture. The Algonquin Highlands is partitioned into 15 WMUs for the purposes of issuing tags and harvest reporting. All hunters were restricted to a maximum of one deer during the study period, and only those with selective harvest tags could take an antlerless (adult female or fawn) deer. The number of tags per WMU was controlled but the number of hunters was not. A firearm harvest was generally run for the first two weeks of November. An archery-only hunt was also run, either for 2 weeks before the regular hunt or for one week before and after the regular hunt.

Data

Harvest data were obtained from the Provincial Mail Survey (PMS) (see Ch. 1). For each WMU (x) and year (t), we used the extrapolated antlerless kill [$\hat{A}(x,t)$], buck kill [$\hat{B}(x,t)$], deer seen [$\hat{S}(x,t)$] and hunters [$\hat{H}(x,t)$] from the PMS, while the number of tags issued [$P(x,t)$] was provided by the OMNR.

The PMS also allowed the calculation of kill rates per hunter for both antlerless (α) and buck kill (β) (/hunter), the estimated proportion of hunters with tags (ρ), the deer seen per hunter (σ), hunter density (per km^2 of forest (L_F)) (θ), and the proportion of the reported total kill (K) that was antlerless (λ) calculated respectively for each WMU (x) and year (t) as;

$$\alpha(x,t) = \hat{A}(x,t) / \hat{H}(x,t) \qquad (3.1)$$

$$\beta(x,t) = \hat{B}(x,t) / \hat{H}(x,t) \qquad (3.2)$$

$$\rho(x,t) = P(x,t) / \hat{H}(x,t) \qquad (3.3)$$

$$\sigma(x,t) = \hat{S}(x,t) / \hat{H}(x,t) \qquad (3.4)$$

$$\theta(x,t) = \hat{H}(x,t) / L_F \qquad (3.5)$$

$$\lambda(x,t) = A(x,t) / K(x,t) \tag{3.6}$$

In Chapter 2, it was shown that deer seen, controlling for effort, was the least likely to be biased index of population density available from OMNR harvest data. Further, log 10 deer seen was linearly related to log 10 effort in a consistent relationship across DMA. Therefore, the number of deer seen by hunters is expected to increase consistently with hunter effort. Any variation from the expected number of deer seen, for a given effort level, will presumably be related to changes in population density (i.e. changes in the deer encounter rate). An index of population was therefore derived by taking the residuals from a linear model of log 10 deer seen versus log 10 effort (d) using data from all DMA.

Statistical Analysis

Data from AH were initially used to test the effectiveness of the selective harvest system. Type I regression was used to fit models of the relationship between the extrapolated antlerless kill in a WMU(x) and year (t) ($\hat{A}(x,t)$) and both the number of tags issued ($P(x,t)$) and the number of hunters ($\widehat{H}(x,t)$). To assess the ability to regulate kill, we fit regression models of the change in antlerless kill (ΔA) from year t to t+1 versus the change in hunters (ΔH), Tags (ΔP) and our index of deer density (Δd) calculated as,

$$\Delta A = \hat{A}(x,t+1) - \hat{A}(x,t) \tag{3.7}$$

$$\Delta H = \widehat{H}(x,t+1) - \widehat{H}(x,t) \tag{3.8}$$

$$\Delta P = P(x,t+1) - P(x,t) \tag{3.9}$$

$$\Delta d = d(x,t+1) - d(x,t) \qquad (3.10)$$

Evidence of limitation of antlerless kill due to deer encounter rates or hunter interference was evaluated by adding σ(x,t) or θ(x,t) to a type I linear regression model of log 10 kill (antlerless or buck separately) versus log 10 hunters.

Relationships determined for AH were then investigated using data from the remaining 7 DMAs to determine the (geographic) generality of the models derived and patterns observed. To reduce sampling errors due to small survey samples, we included only WMUs and years for which at least 20 surveys were returned. Even with this restriction, the number of survey respondents in other DMAs, especially in the northern part of the province, were considerably lower than for the AH (table 3.1).

Results

Historical trends in AH

In the early 1980s, fewer than 10% of hunters in the AH had tags. This level gradually increased through the 1980s, reaching levels of over 50% of hunters for most WMU (as high as 90-95% in some WMU) in the late 1980's and early 1990's. The late 1990s have generally seen tags decline, but not to the low levels of the early 1980s (Fig. 3.1). Total hunter numbers in the AH declined from around 45,000 in the late 1970s to 40,000 during the 1980-1982 period, subsequently increasing to 65,000 in 1989. From 1989, hunter numbers declined gradually to approximately 55,000 in 1996 and 1997, with the exception of a brief spike of 65,000 in 1995 (Fig. 3.1). Total antlerless kill for AH dropped from 4500 deer in the late 1970s to below 1000 in 1980 with the introduction of tags. From 1980-1990, antlerless kill increased to a peak of 14,500, in 1990, declining thereafter to 5,100 deer in 1997 (Fig. 3.1).

Effect of tags and hunter numbers on antlerless kill

Tags issued and total estimated hunters were strongly correlated in the AH ($r = 0.71$). Extrapolated antlerless kill showed a very strong relationship with the number of issued tags (Fig. 3.2a) and a weaker, but still strong, relationship with total hunters (Fig. 3.2b) (Table 3.2). Despite the strong correlation between tags and hunters, both contributed significantly to the fit of a multiple regression model including both terms, with tags having the stronger partial effect (Table 3.2). When the effects of total hunters are statistically controlled, antlerless kill shows a positive saturating relationship with the proportion of hunters with tags $\rho(x,t)$ (Fig. 3.3); above approximately $\rho(x,t) = 0.40$, kill per hunter was essentially independent of the proportion of hunters holding tags.

Since tags restrict only the antlerless kill, the proportion of the total kill that was antlerless (λ) can also be used to assess the range over which tags appear to limit antlerless kill. Presumably tags will reduce λ below what would be achieved in an open hunt (i.e. no tags). The proportion of the kill that was antlerless (λ) also showed a strong saturating relationship with ρ, with the maximum ($\lambda = 0.6$) being achieved at approximately $\rho = 0.40$ (Fig. 3.4). Records for 1977-1979, a period with no tags and therefore an open harvest, had a mean λ (+/-s.e.) = 0.6 +/- 0.1 for all WMU and years in the Algonquin Highlands.

These results suggest that tags restrict antlerless kill only when fewer than 40% of hunters have tags. When data with $\rho < 0.40$ were excluded from the analysis, the relationship between antlerless kill and hunter numbers was considerably stronger than for the whole data set ($N = 104$, $b = 1.127 \pm 0.063$, $t = 20.14$, $p < 0.001$, $R^2 = 0.80$, $RMS = 0.022$) (Fig. 3.5). Tags and hunters were very highly correlated for this data set ($r = 0.95$).

The relative impact of changes in tags and hunter numbers on antlerless kill was assessed by fitting regression models expressing the change in antlerless kill from one year to the next in terms of changes in tags issued, hunter numbers, and the population index $d\Delta A$ was positively related to all three factors; ΔH ($b' = 0.541$), ΔP ($b' = 0.365$) and $\Delta d(b' = 0.207)$ (Table 3). For WMU and years where $\rho(x,t) > 0.40$ and $\rho(x,t+1) > 0.40$, ΔA remained positively related to both ΔH ($b' = 0.527$) and Δd ($b' = 0.354$) but was independent of $\Delta P(b' = -0.022)$ (Table 3.3), a result at least partially due to the dramatic reduction in the range of ΔP (1965 - 2250) for these data compared to the full data set (-5500 – 3965). For $\rho < 0.40$, there was strong positive tag ($b' = 0.559$) and hunter effects ($b' = 0.524$), but a considerably smaller effect of Δd ($b' = 0.134$)(Table 3.3).

Antlerless kill per hunter showed no relationship to tags per hunter beyond $\rho > 0.40$, indicating no tag restriction on kill. Yet for WMU and years with > 40% tag-holders, kill per hunter ranged from 0.02 - 0.36 (mean ±s.d. = 0.17 ± 0.05) for antlerless deer and 0.03 to 0.18 (mean ±s.d. = 0.11 ± 0.03) for bucks, while the reported number of deer seen per hunter ranged from 1.3 to 3.5 (mean = 2.5 ± 0.4). Consequently, the percentage of deer seen that were killed (assuming that all deer killed were reported as deer seen) averaged $12.1 \pm 2.2\%$. These results suggest that factors other than tags may limit hunter success (kill per hunter).

Deer seen per hunter (a measure of deer encounter rates), added to a multiple regression with log 10 hunters, did not show a significant relationship with antlerless kill (b=0.082±0.062, t = 1.32, p = 0.19). However, the results were strongly affected by data from 1984, which was reported to have $\rho(x,t) > 0.4$ for 13 WMU, yet had a lower antlerless kill than buck kill in 11 of 15 WMU ($\bar{\lambda}$=0.40±0.16) and yielded the lowest antlerless per hunter values in this analysis, suggesting tag limitations. When 1984 data were excluded the partial coefficient for $\sigma(x,t)$ doubled and showed a significant, positive relationship with antlerless kill (N = 92, b = 0.173±0.028, t = 6.20, p<0.001). The effect of $\sigma(x,t)$, controlling for hunters, on buck kill (b = 0.201±0.033, t = 6.07, p <0.001) was similar to that for antlerless kill (excluding 1984 data).

Potentially, interference between hunters at high hunter densities may also reduce kill. However, hunter density, when added to the regression model with $\widehat{H}(x,t)$ + $\sigma(x,t)$ (1984 data excluded), had a significant **positive** effect on both antlerless (b = 0.040±0.014, t = 2.78, p = 0.006) and buck kill (b=0.053±0.016, t = 3.23, p = 0.002), meaning kill (per hunter) actually increased at high hunter densities. However, since one forest area value was used for all years in a WMU, the hunter density effect may simply reflect a difference between WMU in mean antlerless kill, controlling for hunters and deer encounter rates. There was a significant WMU effect (F=3.10, df= 11, p=0.002) that when accounted for resulted in non-significant effect of hunter density (F=1.5, df=1, p =0.22) and improved model fit (R^2 = 0.92, RMS = 0.007 vs. R^2 = 0.89, RMS = 0.009).

Relationship between antlerless kill, tags and hunters in other DMA

As in AH, log 10 antlerless kill was positively related to log 10 hunters for the other DMAs, excluding SA (controlled hunts only) combined (N=509, b = 1.21 ± 0.044, t =27.5, $p < 0.001$, $R^2 = 0.60$, $RMS = 0.108$). There was also a strong relationship between log 10 reported antlerless kill and log 10 tags issued (N=369, b = 0.858 ± 0.030, t = 28.0, $p < 0.001$, $R^2 = 0.68$, $RMS = 0.090$).

Again, when hunter numbers were statistically controlled, there was positive, saturating relationship with ρ(x,t), with leveling off occurring at ρ(x,t) >0.40 tag-holders (Fig. 3.6). By DMA results also indicated a limit on the restrictive ability of tags, (Fig. 3.7) for EM, and possibly for CA. In LOW and TB, where tags were almost always > 40%, there was no pattern observed, while SUD, which had few points > 40%, showed a slight negative bias at low tags. There appeared to be a positive relationship between %tags and the residuals for Man, but most of the residuals were positive. No WMU in SA had tags issued as they run a selective harvest.

When only data with > 40% tag-holders were selected (N = 220), the hunter model remained the same but model fit increased (b = 1.25 ± 0.041, t = 29.8, p <0.001, $R^2 = 0.80$, $RMS = 0.054$). There was a significant difference in mean antlerless kill, accounting for hunter numbers, between DMA (including AH) (F= 6.98, df = 6, p <0.001) which improved model fit only slightly ($R^2 = 0.83$, $RMS = 0.039$). A statistically significant difference in the relationship between kill and hunters between DMA (DMA* $\widehat{H}$: F=3.18, p =0.008) added little to the explanation of variance (R^2 =0.84, $RMS = 0.038$).

Discussion

The selective harvest system is based on several assumptions, one of which is that antlerless kill is effectively regulated by tags. The pattern of tags and antlerless kill in Algonquin Highlands superficially appears to support this assumption: low tag numbers in the early 80s appear to have restricted antlerless kill, and increases in total tags issued from 1980 to 1990 were accompanied by a 6-fold increase in estimated antlerless kill from 1983 to a peak of nearly 15,000 deer in 1990. However, hunter numbers also increased dramatically during the same period. Whether this increase was due to perceived increase in hunting opportunities associated with more tags, or if tags were increased in response to higher hunter numbers, is unknown. Regardless, the increased kill was likely the result of a combination of increased hunter numbers, more tags and a large antlerless population resulting from the low harvests in the early 1980s. Declining tags and estimated hunter numbers in the 1990s coincided with a sharp decline in antlerless kill.

These trends notwithstanding, more detailed analysis indicates that if the number of hunters is fixed, increasing the number of tags will increase antlerless kill, only so long as the proportion of hunters holding tags remains below 40%. Above this threshold, issuing more tags will have a negligible effect on antlerless kill. By contrast, irrespective of tag level, annual changes in hunter numbers had a significant effect on annual changes in antlerless kill. When fewer than 40 % of hunters hold tags, changes in hunters and tags had similar effects on the change in antlerless kill. But above 40% tag-holders, changes in antlerless kill were related only to changes in hunter numbers. The results for other DMAs tend to corroborate those found for the Algonquin Highlands and suggest this is a province wide relationship. On an individual DMA basis, only Eastern Midlands and Central Agricultural DMA possessed a sufficient range of tag allocations to demonstrate the same pattern as AH. In CA, kill per hunter, while negative at low tag allocations, was only weakly related to tags per hunter. Lake of Woods, Thunder Bay and Manitoulin had few data points with <40% tag-holders, and demonstrated no significant relationship between kill per hunter and tags per hunter. Sudbury conversely rarely had > 40% tag-holders and its residuals were negatively biased, indicating a lower than expected kill for that number of hunters. In the Southern Agriculture DMA controlled hunts, rather than selective hunts, were utilized mainly for safety reasons. In this region kill was strongly related to hunters, with a model similar to the other DMA.

Taken together, the results for AH and other DMAs suggest that (a) when more than 40% of hunters hold tags, antlerless kill can only be significantly increased by increasing hunter numbers; and (b) even below 40% tags, the most effective regulation of antlerless kill involves regulating both the number of tags and the number of hunters.

Relatively few studies have looked at the effectiveness of selective hunts in regulating antlerless harvest. McCullough et al. (1990) found a strong positive relationship between antlerless kill and tags at the Fort Hunter Liggett military reserve in California from 1967-1982. This 667 km^2 reserve is half the size of the smallest WMU in the Algonquin Highlands, and the antlerless harvest was run on "several" weekends, following 6 weekends of buck only harvest with hunter numbers being limited to 400 per day. The actual number of tags issued was not given by the authors, but was reported as "fairly conservative" (McCullough et al., 1990). This hunt appears smaller and more tightly controlled than those that take place in the Algonquin Highlands.

Even in open hunts, hunter success rate is generally low and in any DMA, in any year, hunter success never exceeded 50 percent. This suggests a strong limitation due to encounter rates, hunter efficiency or hunter behaviour. In AH, both buck and antlerless kill rates were positively correlated with deer seen per hunter, presumably a reasonable index of encounter rates. Therefore, kill was at least partly limited by the number of deer encountered by hunters.

Previous studies of the effects of hunter density on kill have yielded variable results. Foster et al., (1997) found an increase in hunter efficiency with increased hunter density, while Hansen et al. (1986), found evidence of hunter interference. Foster et al. (1997) suggest that the relationship between success and density is non-monotonic: at low densities there are too few hunters to force deer out of hiding, while at high densities there is hunter interference. Higher hunter density may also increase hunter efficiency, perhaps by forcing deer closer to hunters (Kilpatrick and Walter 1999).

In the AH, hunter density (hunters per forest area) had a positive (but relatively small) effect on both antlerless and buck kill, which suggests that at least in the AH, hunter densities are not sufficiently high to produce significant interference effects. Moreover, forest area used to calculate the hunter density is the same for all years within a WMU and accounting for the differences between WMU in kill per hunter, removed the hunter density effect. So the density effect is merely a reflection of improved hunter success in WMU with higher hunter densities, perhaps indicating a tendency for hunters to congregate in higher numbers, and hence higher densities, in WMU where success rates are higher (i.e. flock to known good deer hunting areas).

On average, hunters reported killing only 12% of the deer reported seen. Although a deer seen does not necessarily constitute a chance for a kill, a study on Griffith Island in Georgian Bay found that hunters missed almost a third of all attempts (Holsworth 1973), the large discrepancy between deer seen and kill suggests the possibility of limits due to hunter behaviour. There is some evidence of hunter selectivity in kill, generally favouring adults over fawns and possibly males over females (Roseberry and Klimstra 1974), and since hunters are allowed only one deer, a tag-holder may pass on a fawn or doe, preferring to wait for a buck, thereby lowering overall antlerless kill rates. Hunter selectivity may decrease as the hunt progresses and hunters began to fear not being successful at all (Roseberry and Klimstra 1974). If a large portion of hunters selectivity favour bucks over does, increasing antlerless kill may prove difficult regardless of the number of tags issued or population density.

Additionally, while tags are issued to individuals, hunters often operate in parties, and in the selective system share tags and kills. Regulations banning party hunting were rescinded in 1992, but there is little doubt that even then, party hunting was widespread (Voigt et al., 1992). There may be logistical or hunter demand limits on the number of deer needed per party. When enough deer have been taken to satisfy the group's demand for meat or sport, or exceeds their ability to remove and process kills, the party may act more selectively or no longer actively seek deer. This hunter demand hypothesis would predict that once the limits on kill imposed by tags exceed the hunter demand limit, kill would only increase with increased hunter numbers (i.e. with increased total demand), and the addition of more tags (or increases in deer population) would not lead to increased kill. This is precisely the situation observed for the Algonquin Highlands. A well-designed survey of hunter attitudes and behaviour would allow us to detect any hunter-imposed limit. Deer managers may have to consider actions to change hunter behaviour, such as education or incentives to take more antlerless deer, in order to efficiently manage deer populations.

Taken together, our analyses suggest that while the selective harvest system may be effective at restricting kill to low numbers, it is ineffective in increasing kill to higher levels. Specifically, our results indicate that once the proportion of hunters with tags exceeds about 40%, increased kill can be obtained only through increases in hunter numbers or, possibly, by providing incentives for hunters to take several deer. In many parts of North America, declines in hunter participation and reduction in hunting opportunities are casting doubts on the ability of sport harvests to regulate deer populations (Brown et al. 2000). Problems with deer overabundance, especially in rural areas, may therefore require increased but tightly controlled hunts (i.e. culls) that may have limited appeal to recreational sport hunters (Brown et al. 2000). The OMNR and its managers are already beginning to recognize the limitations of the current harvest system and have introduced changes such as allowing more than 1 deer per hunter, in an attempt to increase harvest in high deer density areas.

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List of Tables

Table 3.1. Sample size and mean survey respondents ($\overline{R}$) (±standard deviation) for WMU and years where the number of surveys returned was ≥ 20, by Deer Management Area (DMA).

DMA	N	$\overline{R}$ (±sd)
Lake of Woods	53	95 (54)
Thunder Bay	37	41 (19)
Sudbury	38	64 (45)
Algonquin Highlands	247	216 (164)
Manitoulian	35	202 (188)
Eastern Midlands	120	156 (116)
Central Agricultural	256	72 (63)
Southern Agricultural	114	74 (39)

Table 3.2. Relationships between estimated antlerless kill ($\hat{A}$) and the number of tags issued (P) and estimated hunter numbers ($\widehat{H}$) for Algonquin Highlands, 1980-1997 for (a) all data and (b) WMU and years where the proportion of tag-holders (ρ) was > 0.40.

Variable	N	b ±*s.e.*	t	P	R^2	RMS
a) All Data						
P	234	0.843 ±0.019	43.34	<0.001	0.89	0.033
$\widehat{H}$	240	1.632 ±0.090	17.99	<0.001	0.58	0.130
P +	234	0.712 ±0.024	29.21	<0.001	0.91	0.027
$\widehat{H}$		0.450 ±0.059	7.65	<0.001		
b) ρ(x,t) > 0.40						
P	104	1.090 ±0.061	17.86	<0.001	0.76	0.027
$\widehat{H}$	104	1.277 ±0.063	20.14	<0.001	0.80	0.022
P+	104	0.267 ±0.178	1.49	0.14	0.80	0.022
$\widehat{H}$		0.988 ±0.204	4.84	<0.001		

Table 3.2. Relationships between estimated antlerless kill ($\hat{A}$) and the number of tags issued (P) and estimated hunter numbers ($\widehat{H}$) for Algonquin Highlands, 1980-1997 for (a) all data and (b) WMU and years where the proportion of tag-holders (ρ) was > 0.40.

Factor	**N**	*b′*	**t**	**p**	**R^2**	**RMS**
All data						
ΔP	220	0.365	7.54	<0.001	0.51	50863
ΔH		0.541	11.18	<0.001		
Δd		0.207	4.28	<0.001		
ρ(t), p(t+1) > 0.40						
ΔP	81	-0.022	-0.25	0.80	0.39	58056
ΔH		0.527	5.89	<0.001		
Δd		0.354	3.97	<0.001		
ρ(t), p(t+1) < 0.40						
ΔP	96	0.559	9.66	<0.001	0.71	26604
ΔH		0.524	8.95	<0.001		
Δd		0.134	2.35	0.020		

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Figure 3.7. The relationship between the residuals from the linear regression of antlerless kill ($\log_{10}$) versus estimated hunter numbers ($\log_{10}$), and the proportion of hunters with tags, by Deer Management Area.

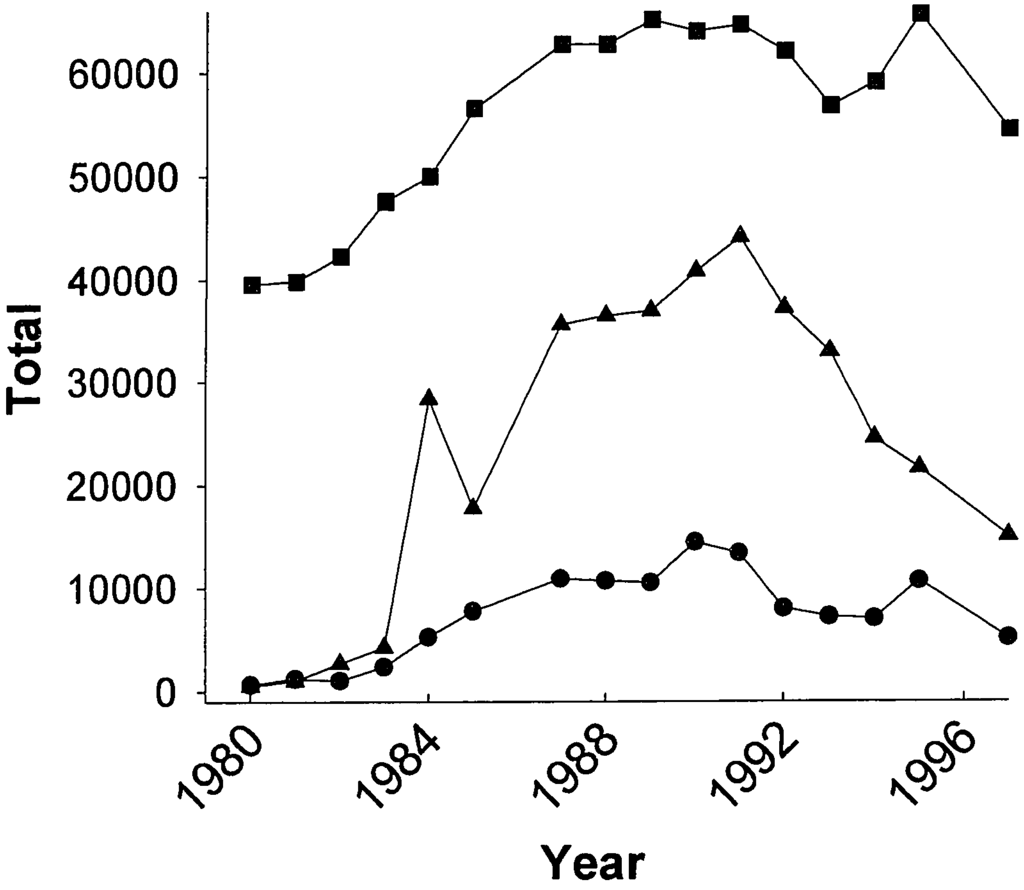

Figure 3.1. Total estimated hunters (■), tags issued (▲), and antlerless kill (●) in the Algonquin Highlands, 1980-1997. The totals for 1986 and 1996 are excluded due to missing WMU data.

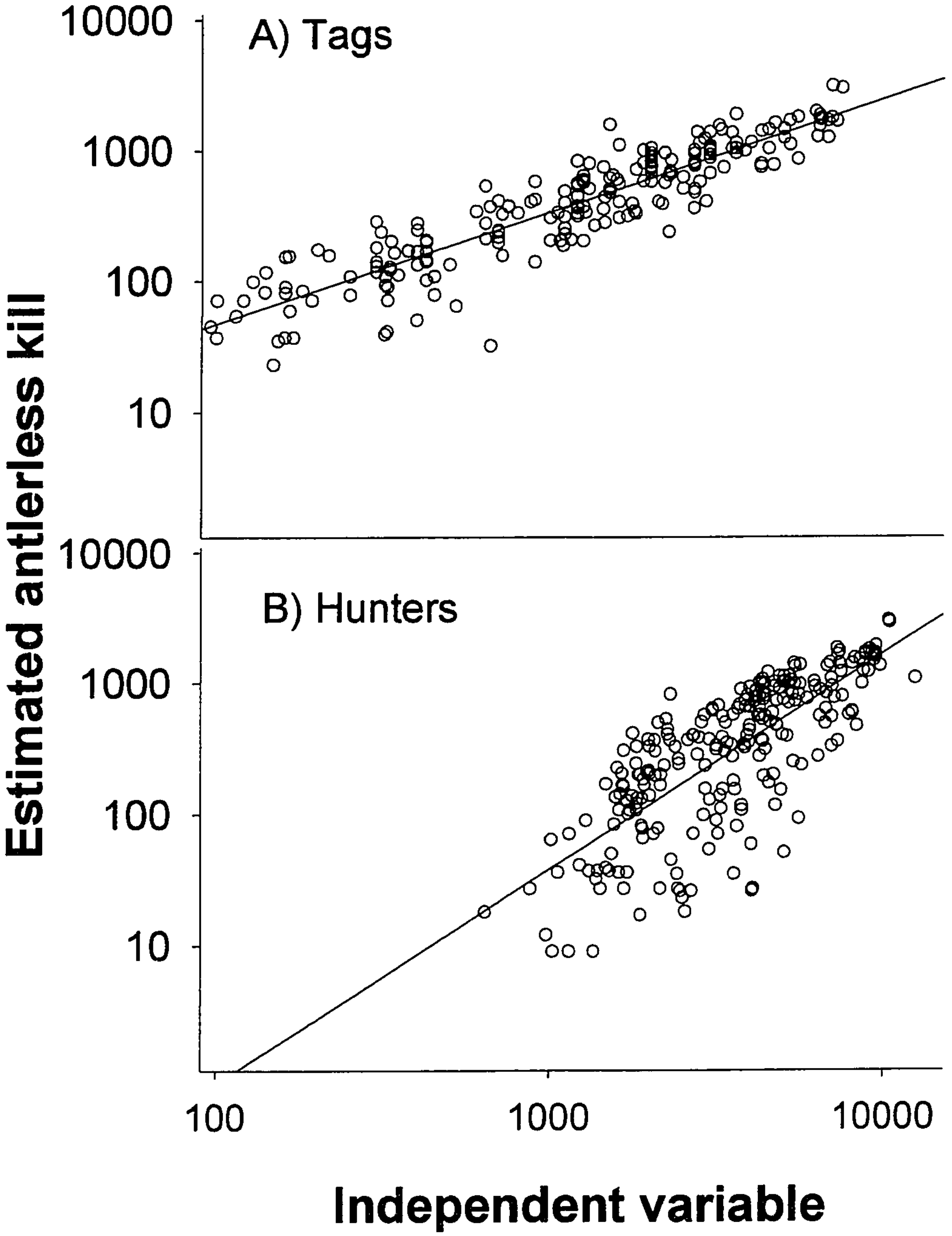

Figure 3.2. The relationship between estimated annual antlerless kill and (a) the number of tags issued; (b) estimated number of hunters, in the Algonquin Highlands, 1980-1997.

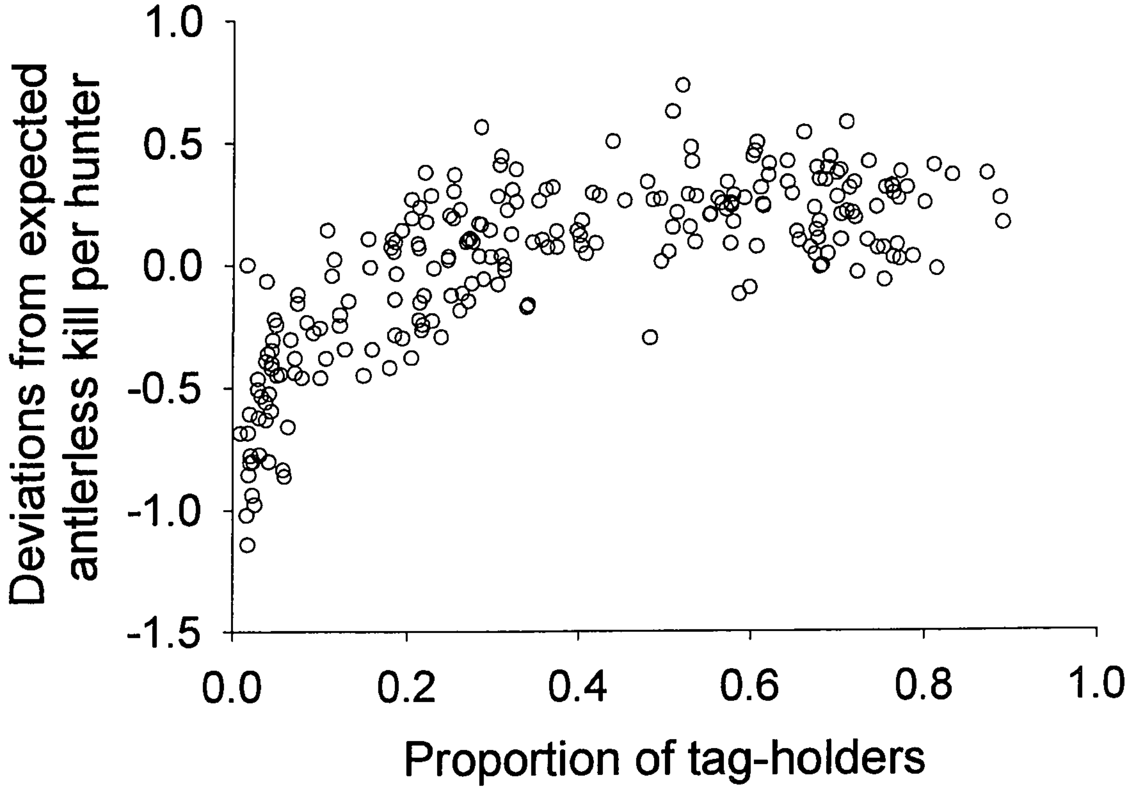

Figure 3.3. Semi-partial plot of the relationship between antlerless kill ($\log_{10}$), corrected for estimated hunters numbers, and the proportion of hunters with tags in the Algonquin Highlands.

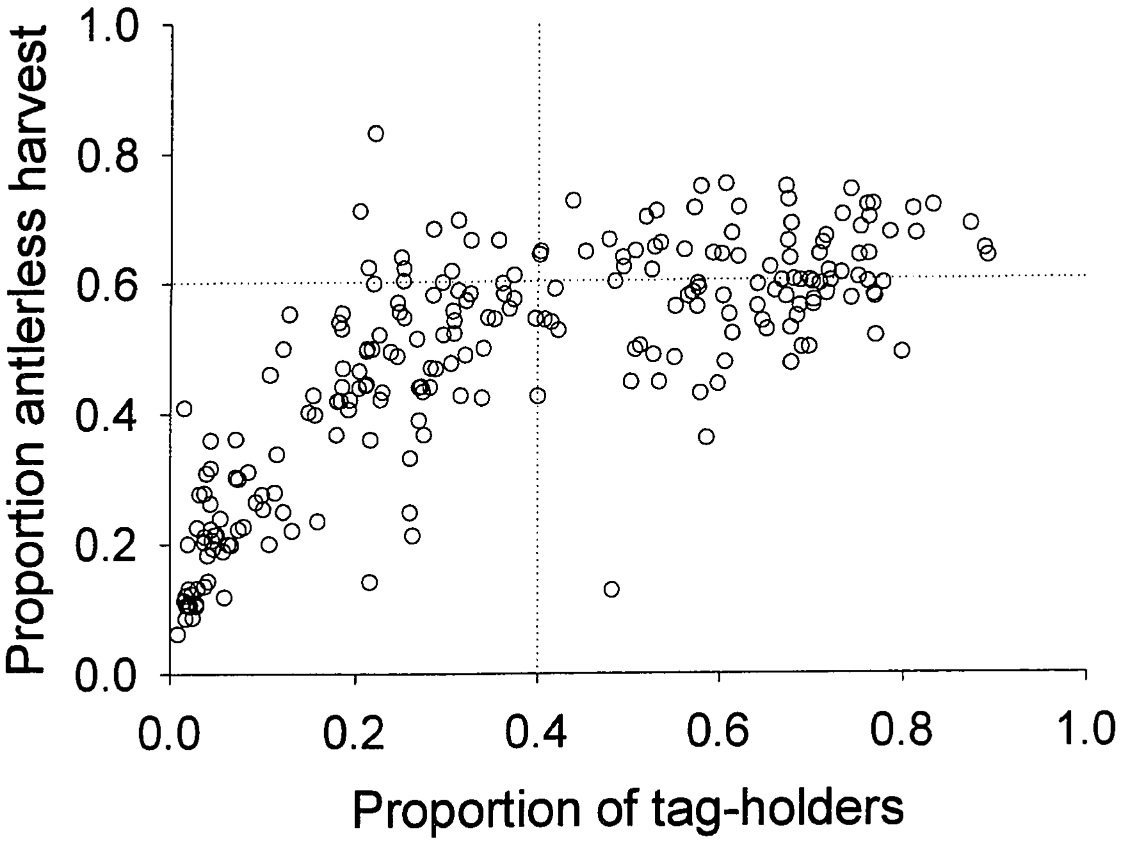

Figure 3.4. The relationship between the antlerless proportion of the harvest (λ) and the proportion of hunters holding tags (ρ) in the Algonquin Highlands, 1980-1997.

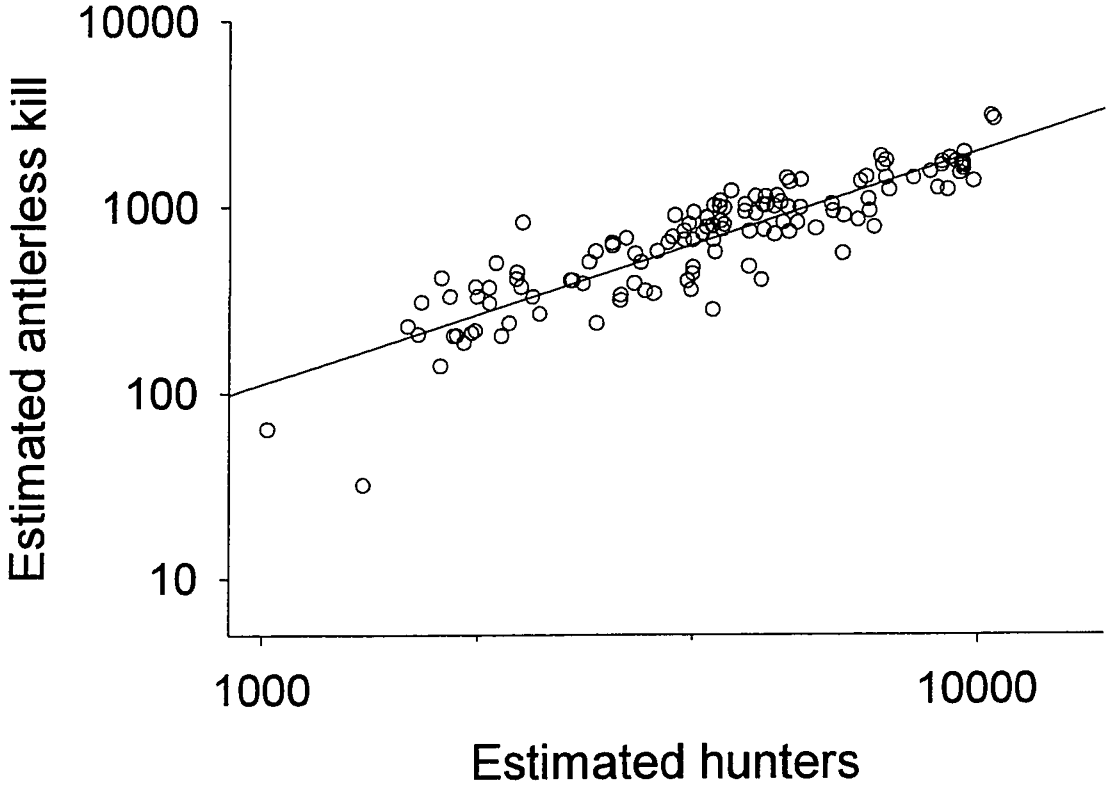

Figure 3.5. The relationship between yearly estimated antlerless kill and the estimated number of hunters for WMU and years with > 40% tag-holders, in the Algonquin Highlands, 1980-1997.

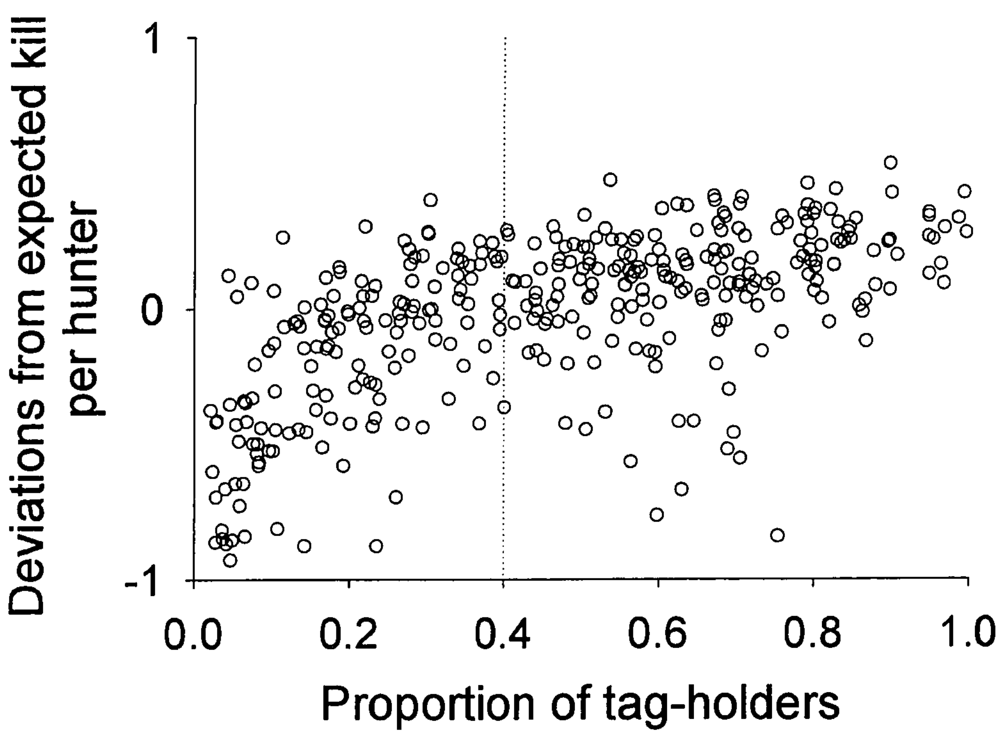

Figure 3.6. The relationship between the residuals from the linear regression of antlerless kill ($\log_{10}$) versus estimated hunter numbers ($\log_{10}$), and the proportion of hunters with tags, for WMU outside the Algonquin Highlands.

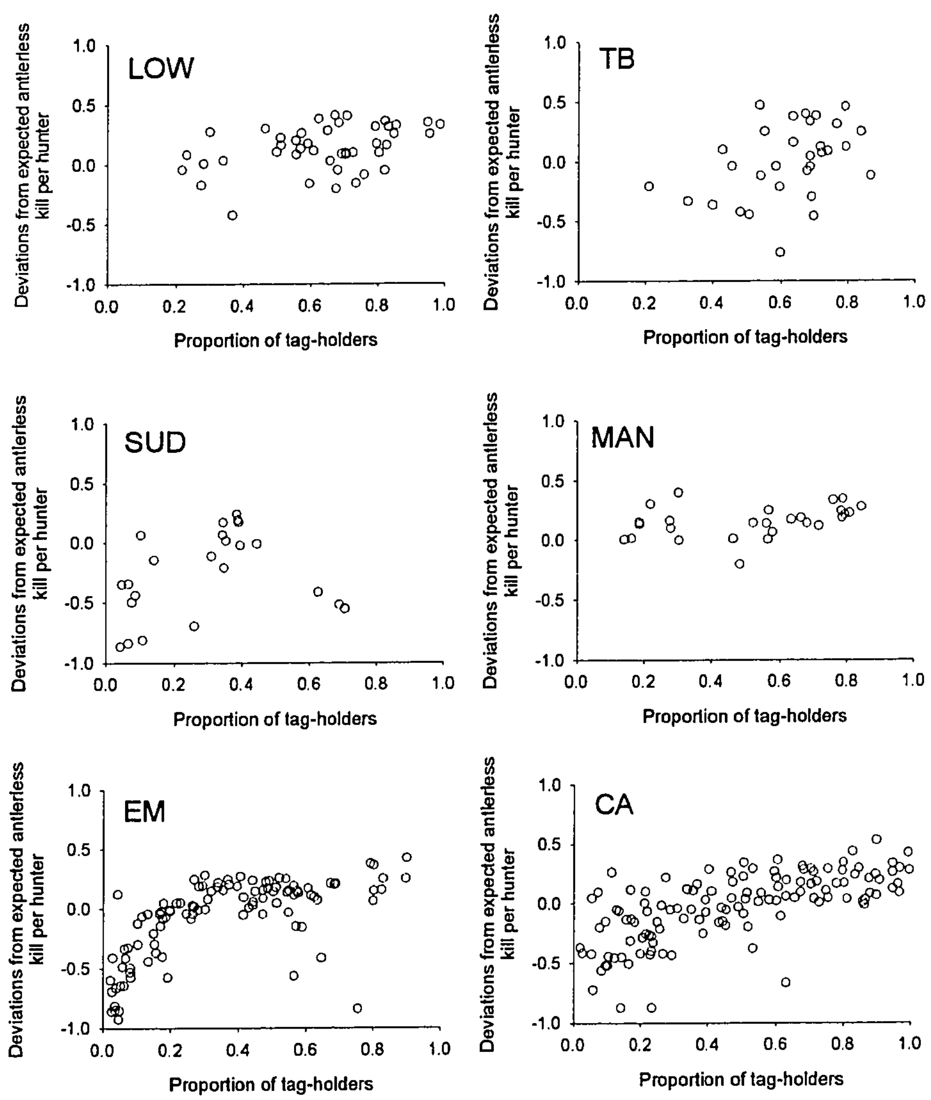

Figure 3.7. The relationship between the residuals from the linear regression of antlerless kill ($\log_{10}$) versus estimated hunter numbers ($\log_{10}$), and the proportion of hunters with tags, by Deer Management Area.

Chapter 4: Regulation of white-tailed deer populations in the Algonquin Highlands Deer Management Area, Ontario.

Introduction

The management of white-tailed deer (*Odocoileus virginianus*) in Ontario has for decades been based on two assumptions: that (a) the selective harvest system, through the issuing of antlerless deer harvest tags, regulates antlerless kill; and (b) deer populations can be effectively regulated through changes in antlerless kill. In Ch. 3, I showed that historically the size of the antlerless kill was, to a large extent, regulated by tags when the proportion of hunters having tags was low, but above 40% tags, kill was independent of tags. By contrast, irrespective of the proportion of hunters having tags, changes in hunter numbers had a direct and predictable effect on kill, suggesting that the direct regulation of hunter numbers may be a more effective way of managing kill.

Clearly, assumptions (a) and (b) above are independent. Consequently, even if we had an effective way of regulating antlerless kill, this will not be effective in managing deer populations unless antlerless kill has a strong (down-) regulatory effect on population density. Unfortunately, determining the (true, as opposed to inferred) population dynamics of white-tailed deer has long been a challenge for wildlife managers. Most harvest management plans are meant to respond to (real or perceived) changes in deer populations, but accurate and reliable measures of population size and/or density are not usually available. Consequently, deer managers usually base management decisions either on (1) changes in (putative) indices of population; or (2) events that are assumed to exert strong -regulatory effects in the specific population(s) being managed (e.g. severe winters or large harvests).

If kill is to exert a strong, predictable and reliable impact on deer populations, then other factors which, in principle, influence population dynamics must either (a) exert relatively small effects; or (b) exert pressures whose both marginal and interactive effects with kill can be reasonably well estimated. Such factors include those influencing immigration and emigration, natural mortality, and fecundity.

Annual population change will be determined by (reproduction + immigration) – (mortality + emigration). Measures of immigration and emigration rates are generally unobtainable, but on a large scale are generally assumed to be balanced and therefore of little importance in determining population change. Deer in northern climates show fidelity to their migration routes between summer habitats and winter habitats or "yards" (Nelson and Mech, 1981; Tierson et al. 1985), with offspring apparently learning migration routes from their mothers (Nelson and Mech 1981). Yearling males are believed to disperse, and movement in excess of 20km from their natal areas was observed for radio-tracked yearling males at Chesapeake Farms, Maryland, though the estimated level of emigration (N = 39 ± 8 yearling males) was offset by a similar level of immigration (N = 31 ± 11) (Rosenberry et al., 1999). A study of red deer (*Cervus elaphus*) concluded that emigration played no significant role in population regulation (Clutton-Brock et al. 1985).

Hunting and predation (wolf, coyote, bear, dog, etc.) are considered the major sources of mortality for deer populations in northern climates (Nelson and Mech 1986, Fuller 1990, Van Deelen et al. 1997, Whitlaw et al. 1998, Dumont et al. 2000). Other significant sources of mortality include malnutrition due to harsh winters, illness and vehicle collisions (Kucera 1976, Van Deelen et al. 1997, Dumont et al. 2000). Natural (i.e. non-hunting) mortality rates apparently vary between ages and sexes, with fawns suffering overall larger mortality than adults (Clutton-Brock et al. 1985, Nelson and Mech, 1986, Dumont et al. 2000). Harvest mortality appears greatest for young adult males, especially in harvest systems where antlerless kill is restricted, and is usually attributed to their inexperience and higher dispersal rates (Nelson and Mech 1987, Van Deelen et al., 1997). While harvest mortality can be relatively easily recorded or estimated from hunter surveys or check stations, natural mortality is often difficult to estimate directly and is instead often assessed on the basis of proxy measures (indices) such as physical condition or weather conditions.

Reproductive rates are also difficult to estimate as newborn fawns are rarely seen. As deer must reach a certain body size to breed (Severinghaus and Moen, 1983), physical condition is an important determinant of the number of breeding individuals, the reproductive rate (i.e. embryos per deer) and the timing of conception, the latter of which can affect fawn survival (Severinghaus and Moen, 1983, Langvatn et al. 1996). Physical condition is in turn related to weather conditions and habitat quality. Deer forage from spring until fall in order to replenish reserves lost during the winter, to nurse fawns and to achieve sufficient body size to breed in the fall and survive the winter (Voigt et al. 1992). In addition to direct adult mortality and intra-uterine loss of fawns, a major effect of harsh winters is post-natal mortality of underweight fawns in the spring (Verme, 1977). Moreover, both mortality and reproductive rates show density-dependence in white-tailed deer and other cervids; consequently, population density is another factor that must be considered in population management (Messier et al., 1991, Albon et al., 1987, Clutton-Brock et al., 1985, McCullough, 1979).

Estimates of mortality and reproduction may be obtained from harvest indices or other surveys (e.g. fawn: doe ratios, dead deer surveys). Alternatively, they may be obtained indirectly by collecting data on the factors thought to regulate them. Both mortality and reproduction are, at least in some circumstances, related to a variety of interacting factors such deer physical condition, habitat quality, climate, predation and population density. Some of these factors can be measured directly (e.g. climate) or can themselves be estimated or assessed by reference to specific (putative) indices (e.g. yearling physical condition in the fall as an index of habitat quality during the preceding summer)

Relatively sophisticated population models have been developed to predict deer population changes from estimates of mortality and recruitment or their (putative) controlling factors (e.g. Broadfoot and Voigt 1992, Jensen 1994, Xie et al. 1999). Most of these models either require data not generally available and/or expensive to obtain with the required accuracy and precision (e.g. detailed age/sex population structure, forage quantity/quality estimates, etc.) or are based on relationships determined for other geographic areas. Both constraints undermine the practical utility of such models for deer managers.

A complementary approach is to use existing data to develop statistical population models that make predictions about deer population changes in general, and more specifically, about the impacts of management interventions thereon. This approach has several advantages: (1) it allows for a quantitative (or at least semi-quantitative) assessment of the reduction in predictability associated with model simplification, compared to the savings in resources associated with collecting the data required for more sophisticated models; (2) it allows particular hypotheses about the factors influencing deer population dynamics to be tested for the specific geographical areas of management concern; (3) it can in principle identify the cost, in terms of reduced predictive power, associated with using "general" (i.e. mean-field) relationships fitted over large geographical areas to smaller sub-areas, thereby identifying potential resource savings (i.e. using a general model results in small changes in predictive power at smaller spatial scales, compared to that obtained from a model specific to the area in question) or necessary resource expenditures (i.e. large reductions in predictive power, implying that effective management at smaller scales requires data be collected at such scales); (4) it increases the (a priori) practical utility of the models by virtue of their (relative) simplicity and, consequently, ease of access and implementation.

From existing data sources we can statistically estimate the effects of several variables that may influence deer population dynamics, including (1) demographic (age and sex structure) variables; (2) harvest variables, (3) environmental weather variables and (4) variables representing physical condition. An index of local population density, the number of deer seen by hunters controlling for effort, was used to investigate the relationship – if any- between these variables and annual changes in the population index. Specifically, we constructed simple statistical models relating these annual changes within a specific geographic area, to demographic characteristics of the deer population, the harvest, environmental conditions and physical condition. In doing so, we had two related objectives: (1) to use existing data to test specific hypotheses concerning the effects of certain factors on deer population dynamics; and (2) to assess the predictive power of such models and, as such, the implications of their use to both deer and hunter management.

Methods

Study Area and Data

For the purposes of wildlife management, Ontario is divided into Wildlife Management Units (WMU) and harvest is regulated at the WMU level. Those WMUs that allow deer hunting are combined into 8 Deer Management Areas (DMA) based on habitat and climate (see Ch.1). This study used data from the Algonquin Highlands (AH) DMA, one of the most heavily hunted areas in the province.

The number of deer seen by hunters is related to the (local) deer population densities, spatial distribution, hunter effort, and deer visibility (as a function of weather, habitat and terrain). In chapter 2, we showed that there is a strong linear relationship between the reported deer seen (*S*) and reported hunting effort (*E*) for all WMU (*x*) and years (*t*) in the AH ($b = 1.02 \pm 0.02$, $t = 54.13$, $df = 245$, $p<0.001$, $R^2 = 0.92$, $RMS = 0.009$), and that other variables that might be expected to influence deer seen (such as hunter density, weather conditions during the hunt and habitat type) explained negligible amounts of observed variation. Hence, the difference between the expected number of deer seen based on effort, and actual number of deer seen should be related to population density. Accordingly, we used the residuals (d) from the linear regression of;

$$\log_{10} \mathrm{S} = \mathrm{c} + \log_{10} \mathrm{E} \qquad (1)$$

where S is the estimated deer seen and E is hunter effort, for all WMU and years, as our index of population. Our index of annual changes in population density is the change (Δ) in the residuals (*d*) for WMU (*x*), from harvest year *t* to year *t+1*:

$$\Delta d(x)_{t \to t+1} = d(x, t+1) - d(x, t). \qquad (2)$$

Under this formulation, $\Delta > 0$ (< 0) implies that between t and t + 1, deer population density within a particular WMU increased (decreased).

Our objective was to build statistical models that predict Δd as a function of changes in other variables that might reasonably be expected to influence population dynamics. Explanatory variables included those associated with the harvest itself, weather conditions, and (putative) proxy measures of reproduction. Harvest variables were taken from the Provincial Mail Survey (PMS) and included the extrapolated total ($\hat{K}$), buck ($\hat{B}$) and antlerless ($\hat{A}$) kill (see Ch. 2 for detailed description). Weather data were obtained from the Canadian Daily Climate, Eastern Canada 1998 CD-ROM published by the Climate Products and Publishing Division, Climate and Water Systems Branch, Environment Canada, as previously described (see Ch. 1). Daily total precipitation and average temperature data were used to calculate the following variables for each WMU (x) and year (t);

a) $R_P(x,t) \equiv$ total rainfall from April to May (spring)
b) $R_S(x,t) \equiv$ total rainfall from June to August (summer)
c) $T_P(x,t) \equiv$ average daily temperature, April – May (spring)
d) $T_S(x,t) \equiv$ average daily temperature, June – August (summer)
e) $T_W(x,t) \equiv$ average daily temperature, November – March (winter)

The Snow Network for Ontario Wildlife (SNOW) provided another measure of winter severity (Ws), the snow depth index (SDI) calculated as the cumulative snow depth for the entire winter (cm), measured at a series of stations across the province. For each WMU (x) and harvest year (t), *Ws* was taken from the most representative station or an average of multiple stations as designated by the OMNR (Warren et al., 1998).

Mean yearling antler beam diameter (YABD) ($\bar{Y}$) for each WMU and year was extracted from the OMNR Big Game Mortality files (BGM). These measures have been used as indices of summer climate conditions and forage quality (Voigt et al. 1992) and for estimates of fecundity (Severinghaus and Moen, 1983), although the strength of these (putative) relationships in Ontario and their general applicability is largely unknown. Recruitment was measured by the fawn: doe ratio (FD) and was taken from both hunter surveys (PMS) (FD-H) and at check stations (BGM) (FD-C), and reproductive measures included the proportion of lactating does (LD) and the average number of embryos per doe ($\overline{ED}$) measured at hunter check stations and available in the BGM.

Hypotheses and Statistical Analysis

The available data allow us to test three specific hypotheses about deer population regulation: (1) the hypothesis that deer populations are, at least to some extent, subject to density-dependent regulation predicts a negative relationship between Δd and d at previous time periods; (2) the hypothesis that hunter kill exerts a significant (down) regulatory effect on population growth predicts a negative relationship between Δd and harvest in year t; (3) the hypothesis that weather conditions, through effects on recruitment and mortality, will have some predictable effect on population growth.

Type I bivariate and multiple regressions were used to determine the relationship between $\Delta d(t, t+1)$ and measures of population size, weather, recruitment, the harvest and first order interactions between them for each WMU(x) and year (t). Time lags were investigated by fitting models of the change $\Delta d(t, t+1)$) as a function of predictors at times t-1, t-2, t-3 and t-4, and the 2,3 and 4 year cumulative sums and averages. The categorical variable WMU and the interactions with WMU were included in the models to assess the scale of geographical variation in model behavior.

The best overall model to predict Δd was selected using stepwise (backwards and forwards) regression (p entry/removal =0.15).

Results

Temporal trends in the population index

Mean d for AH (averaged over WMUs) increased sharply from 1980 to 1984, declined through the late 1980's and early 1990's reaching a nadir in 1992, increased again from 1992 – 1995 and subsequently declined (Fig. 4.1). In comparison, mean kill per unit effort (KPUE) increased steadily from 1980 to 1991, and has subsequently declined.

Factors regulating population

Density Dependence and Recruitment

Deer populations in AH showed evidence of density-dependent regulation, namely a significant negative bivariate relationship between the change in population ($\Delta d(t, t+1)$) and the population size in year t ($b = -0.494 \pm 0.056$, $t = -8.73$, $p < 0.001$, $R^2 = 0.25$, $RMS = 0.006$) (Table 1) (Fig. 4.2). The previous year's population index, $d(t-1)$, when combined with d(t), had a significant positive effect on Δd (b=0.196 +/- 0.070, t = 2.77, P=0.006), but only slightly improved model fit ($\Delta R^2 = +0.02$, $\Delta RMS = -0.0001$). No relationships between Δd(t) and d(t-j) were detected for j > 1.

There were no significant correlations between any of our estimates of deer reproductive rates; fawn: doe ratios, from hunter surveys (*FD-H*) and from check stations (*FD-C*), $\overline{ED}$ and *LD* (Table 4.2). No estimate for harvest year t +1 (which reflects recruitment from year t to t+1) showed any significant relationship to population in year t that would indicate a density-dependent effect on reproductive rates (*FD-H*: b = 0.05±0.18, $t = 0.29$, $p = 0.76$; *FD-C*: b = 0.07±0.13, $t = 0.58$, $p = 0.56$; $\overline{ED}$: b = -0.26±0.55, $t = -0.48$, $p = 0.63$; *LD*: b = 0.16±0.12, $t = 1.39$, $p = 0.16$). Nor was there a significant relationship between $\Delta d(t,\ t+1)$ and any measure of recruitment in year t+1or reproductive rates from the previous breeding season (Table 4.1).

There was no evidence of a density-dependent effect on mean YABD ($\overline{Y}$) in AH for those WMU and years where data was available (N=77, b = -0.001±0.05, $t = -0.022$, $p = 0.98$, $R^2 = 0.00$). However, a negative relationship was observed between $\overline{Y}(t+1)$ and *d(t)* (N =24, b = -0.063±0.029, $t = -2.18$, $p = 0.04$, $R^2 = 0.17$, $RMS = 7.41$),), for two southern WMU where YABD was recorded annually (WMU 85: 1980-1989; WMU 93:1982-1997) for a relatively large number of yearling deer ($\overline{N}$ =25 ± 12). A stronger relationship was observed with the 4-year cumulative population size (sum of *d(t)...d(t-4)*) (N = 18, b = -0.07 ±0.01, $t = -5.81$ $p < 0.001$, $R^2 = 0.72$, $RMS = 3.03$). This may indicate a density-dependent response in physical condition, resulting in smaller physical size at high population densities.

Harvest

There were statistically significant, but weak, negative individual relationships between Δd and (a) extrapolated total kill and (b) extrapolated antlerless kill, but not buck kill (Table 1). Antlerless kill is highly correlated with total kill ($r = 0.931$), but less so with buck kill ($r = 0.782$). After accounting for the effect of population size in year t and t-1, there was a marginally significant negative effect of extrapolated antlerless kill ($b = -0.016 \pm 0.008$, $t = -1.95$, $p = 0.05$) that resulted in only a small improvement in model fit ($R^2 = 0.28$, $RMS = 0.0061$ versus $R^2 = 0.27$, $RMS = 0.0062$).

The downward regulation of kill may operate only beyond a threshold value when a certain proportion of the population is removed, presumably when kill is greater than recruitment. Therefore, kill in relation to population, rather than absolute kill, may be a better measure in testing for an effect of kill. However using the first order interaction between $\hat{A}(t)$ and $d(t)$ did not yield a better model ($R^2 = 0.24$, $RMS = 0.006$) than the individual effects model ($R^2 = 0.26$, $RMS = 0.006$). Antlerless kill per deer sighted showed a negative effect on Δd, after accounting for population size in year t and t-1 ($b = -0.444 \pm 0.190$, $t = -2.33$, $p = 0.021$) that while marginally better than antlerless kill, still added little to model fit ($R^2 = 0.29$, $RMS = 0.0060$).

Weather

Of the six weather variables examined, only total spring rain and average summer temperature (positive) and SDI (negative) in year t showed statistically significant bivariate relationships with Δd, with no single variable having a total R^2 greater than 0.08 (Table 4.1).

Weather variables, in year t, t-1, t-2 and t-3 were added to model with $d(t)$ and $d(t-1)$ to determine the effects of weather (+ possible lag effects) after accounting for the population effect (Table 4.3). Spring rain, summer temperature and SDI in year t

remained statistically significant and there were statistically significant effects of T_P(t-1), T_S(t-1), T_W (t-2) and W_S(t-2). Statistical significance must be interpreted cautiously, in light of the number of regressions run, and more importantly none of the effects greatly improved model fit, with the largest effect observed ($R_P(t)$) accounting for only an additional 6% of the variation explained (Table 4.3). Since the effects of weather may be related to population, first-order interactions between $d(x,t)$ and each of the weather effects in year t were added to the population and kill model (Table 4.3). None of the interactions with population were significant (all $p > 0.05$) and did not explain any extra variation in Δd.

Predicting annual changes in the deer population index

The best overall model to predict population change included $d(x,t)$, $d(x,t\text{-}1)$, antlerless kill, summer temperature from year t and $t\text{-}2$, spring temperature from $t\text{-}1$ and SDI from t and $t\text{-}3$ ($R^2 = 0.46$, $RMS = 0.005$) (Table 4.4). Our index of population size in year t had the largest effect size in predicting Δd, while the individual effect sizes of the other variables were small (Fig. 4.3) and only combined did they yield a significant contribution to the explanation of variation in Δd, above that explained by $d(t)$ alone ($R^2 = 0.25$, RMS = 0.006). After accounting for all the relevant population, harvest and weather variables there was no difference in the mean Δd between WMU ($F = 1.22$, $df = 13$, $p = 0.22$). Even when only $d(t)$ is accounted for, the difference between WMU while significant ($F = 2.11$, $df = 13$, $p = 0.01$), did not account for much of the variation in Δd ($R^2 = 0.33$, $RMS = 0.006$). Further, there was no evidence of differences among WMU in the nature of the density-dependence ($WMU{*}d(t)$: $F = 0.57$, $df = 13$, $p = 0.87$). The lack of a WMU effect is not a surprising result. While population size varies significantly between WMU, using the annual change in population as the dependent variable will remove much of the variation.

Empirically, the predictive capability of the model, assessed by plotting the predicted versus observed values, was poor (Fig. 4.4), as indicated by the spread of data. A more detailed assessment of the predictive ability of this population model, and its usefulness for management purposes, is carried out in Chapter 6.

Discussion

Factors regulating population

The negative relationship between Δd and d in AH, a pattern consistent with the hypothesis of density-dependence, has also been observed in white-tailed deer in other regions (Patterson and Power 2002, Messier 1991; McCullough 1978), moose (Messier 1991) and elk (Coughenour and Singer, 1996) and many population models include density-dependent effects (Jensen 1995; Saether et al. 1996).

Population declines at higher population densities are often attributed to lower productivity and/or higher natural mortality due to competition for forage. Both fecundity and deer physical condition, which is thought to control fecundity, have in some instances shown negative relationships with population density (Fryxell et al. 1991, Leberg and Smith 1993, Swihart 1998). However, we detected no relationships between measures of reproductive rates and population size that would indicate changes in productivity and/or recruitment were the causal mechanisms behind the observed density-dependence.

While not observed in AH, data from other WMU suggested that YABD had a negative relationship with population that may be strongest when the effects of up to the previous 4 years population densities were considered. A negative relationship between antler beam diameter and population was documented in the Canonto deer yard in Ontario (Lambert et al., unpubl.) and in other areas of North America (McCullough, 1979). Smaller antler beam size at high population densities may indicate a reduction in overall physical condition, which has been linked to lower reproduction (Severinghaus and Moen 1983, Verme 1969) and higher fawn mortality (Verme 1977).

Physical condition may also affect adult survival rates, though this has not been strongly documented. Dumont et al. (2000) concluded that in the absence of hunting, deer in an area of southeastern Quebec were regulated by winter mortality due to competition for forage. Density-dependent winter mortality was also identified as the key factor in population regulation of red deer (Clutton-Brock et al. 1985). As there were no direct measures available, we could not determine if natural mortality (winter or summer) was the causal mechanism behind the observed density-dependent relationship.

Historically at least, our analysis indicates that in the AH, the annual harvest has, generally had only a mild (down) regulatory effect on deer populations, at least at the level of the WMU. Fryxell et al.(1991) found a negative relationship between hunter effort in year t and net annual rate of increase (N_{t+1}/N_t) for the Canonto deer population in southeastern Ontario, using a population estimate derived from harvest records by cohort analysis. Intensive harvests or culls have been successfully used to achieve reduction in deer density for relatively small areas (Roseberry et al. 1969, McCullough 1979, Kilpartick and Walter, 1999). However, the effectiveness of harvest as a long-term control measure for large geographic areas has not been well documented, and doubts have been raised about the efficacy of harvest as a management tool (Brown et al. 2000).

The lack of a significant regulatory effect of harvest in the AH is supported by the fact that AH harvest continued to increase after the population index peaked and declined in the 1990s, suggesting that kill was limited more by tags and hunter effort than population in the 1980s. The sharp drop in the mean population index, following high harvests in 1991 and 1992, may demonstrate that harvest must exceed some threshold, in relation to population size, before causing declines. However, neither the first-order interaction between antlerless kill and population size nor kill per deer seen, attempts to express kill as a proportion of population, showed any significant effect on population. It would appear that for most of the study period, harvest was not sufficient to down regulate population.

None of the individual weather variables studied were strongly related to population change, though a combination of variables, over time, appeared to exert some effect. Winter severity, which is generally believed to be an important determinant of mortality and recruitment, was surprisingly not a significant factor in predicting population change. Deer populations in northern climates live at a higher percentage of carrying capacity in the winter than summer, due to reduced habitat use during "yarding" and the poor quality of winter forage (Voigt et al., 1992). Winter mortality, due to starvation and predation, is cited as the second most abundant source of mortality, after hunting, in many studies (Nelson and Mech 1986, Fuller 1990, Dumont et al. 2000, Lamoureux et al. 2001). In addition, winter severity is often associated with both in-utero and post-natal fawn mortality (Verme, 1977).

The snow depth index showed only a weak negative effect on population change, while winter temperature was not a significant factor at all. Nor was there evidence of an interaction between population and snow depth that might be expected if winter effects were themselves density-dependent, in response to increased competition for food or habitat. Numerous studies have shown negative effects of deep snow on fawn survival (Kucera 1976, Verme 1977, Picton 1984, Mech et al. 1987), though few studies have shown a relationship between snow depth and population change (Mech et al. 1987, Patterson and Power 2002). Severe winter conditions are often blamed (along with over harvest) as the cause of apparent population declines in the 1970's that lead to the introduction of the selective harvest (Voigt et al. 1992). Snow depth in the 1980's was significantly lower than in the 1970's, which may account for the lack of a significant SDI effect.

Deer populations showed slightly stronger relationships to spring/summer conditions, with increases following warm summers and cool/wet springs. Presumably the effects of spring/summer weather on population size are related more to physical condition going into the breeding season and winter, which in turn affects productivity and winter survival, than direct summer mortality, generally thought to be minor in northern populations (Voigt et al. 1992, Dumont et al. 2000). Spring/summer weather conditions that increase the availability and quality of forage for deer have been shown to increase both fawn survival (Albon et al. 1987) and reproductive ability in the fall (Langvatn et al. 1996). However, our limited YABD data did not demonstrate any relationship between physical condition and population change. Like snow depth, the effects of spring/summer weather may also be related to population density, though statistically we found no evidence of interactions with population. A variety of interacting weather conditions, acting with time lags, may have some role in deer population regulation, but their combined contribution to the model was minor, especially in comparison to the complexity they added to the model.

Productivity data (embryos per doe, % does lactating), recruitment data (fawn: doe) and measures of physical condition (YABD) measured at the WMU level were not significant in predicting changes in population into the following year. It seems unlikely that recruitment would have no effect on population regulation, and our findings likely reflect a poor ability to accurately measure productivity on the correct scale, rather than a lack of a biological relationship. The accuracy of the productivity data collected at check stations is suspect due to small sample sizes (Bellhouse 1993). An analysis of check station data indicated that variation in YABD, as measured at check stations, was greater within a WMU and year than between WMU and years and therefore may be poor indicators of yearly changes in physical condition (unpubl. data). Fawn: doe ratios from the hunt are potentially poor measures of actual recruitment due to hunter selectivity, favouring adults over fawns, and sex/age differences in vulnerability to hunting (Coe et al. 1980, McCullough et al, 1991). Harvest survey recruitment data are also potentially further biased by the presumed tendency of hunters to report fawns as does, and empirically reported fawn: doe ratios are generally lower than those measured at check stations for the same WMU and year (pers. obs.).

Management use of the model

Overall, the best model, which incorporated 8 independent variables, explained less than half the variation in the change of the population index. As a result the ability of the model to predict even the data it was built from was empirically poor. One would assume that its ability to predict future data points would be even worse, especially in light of possible changes in climatic conditions. The poor predictive ability of our model could be the result of any combination of; (a) poor relationship between our index of population (deer seen controlling for effort) and actual population size, (b) omission of other important factors not measured, (c) data were not measured accurately or at the correct scale, (d) no biological relationship between the factors measured and population size or (e) deer populations are inherently stochastic. We have no way of determining which of the above reasons account for the lack of relationship.

Realistically, we are not collecting all data that are potentially important to deer population regulation. For example, no data are available in Ontario on the level of predation by wolves and coyotes, which has been shown to be significant source of mortality, though its role in population regulation has been debated (Messier 1991, McRoberts et al. 1995). Not having a systematic, collection method for productivity or recruitment data is another notable omission given its obvious role in population regulation. Most recruitment data come as a by-product of other surveys (i.e. fawn: doe), is collected sporadically (embryo per doe, lactating does) or is measured indirectly through factors thought to alter productivity or fawn survival (e.g. physical condition, winter severity, spring/summer conditions).

However, without a direct measurement of population against which to determine the accuracy of our index of population, there is no guarantee that the collection of any new or better data will improve our ability to predict changes in population. We could accurately be measuring all the factors that regulate population, but if our index of population does not relate to actual population then our model will not detect their effects.

Regardless of the reasons behind the poor predictive ability, the management implications of the model remain the same. Despite the considerable effort spent to acquire deer biological and harvest data, we are unable to determine what effect, if any, changes in harvest will have on deer population. Either harvest, at the levels currently experienced, has no regulatory effect on deer populations or the data currently collected do not allow us to detect the effect. If the former is true, it would question the usefulness of the sport harvest as currently operated, in regulating deer populations. While the latter would question the usefulness of continuing to collect data which do not provide any guidance to deer managers in setting harvest levels.

If our index of population is indeed related to actual population, our model indicates that deer are self-regulating through density dependent processes, and are not being affected by kill. Further, the lack of a significant difference between WMUs suggests that these findings are consistent across the Algonquin Highlands. The ability of the sport harvest to regulate deer populations has been questioned in other areas, especially in light of deer overabundance problems and declining hunting participation (Brown et al., 2000). In 2001, some WMU in southern Ontario began issuing more than one kill permit per hunter, in recognition that past harvests were insufficient to check deer population growth (Margaret McLaren, OMNR, pers. comm.).

However, our inability to find a significant kill effect may also stem from the high degree of "noise" in our data obscuring the kill "signal". In such a scenario, either the data collection must be improved to reduce the noise, or changes in kill must be large enough to produce a large, detectable signal. There is no point, from a population regulation point of view, in applying small changes in harvest, since with current data we have little chance of predicting or evaluating the resulting change in population. At some level, deer harvest must have the ability to suppress population and future kills may need to be increased to reach desired population levels. Whether this level can be reached through a sport harvest would be another issue to be resolved. This study indicates a need to review current population management and data collection systems in the Algonquin Highlands.

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List of Tables

Table 4.1. Bivariate relationships between individual predictor variables and the change in population index between years t and t + 1(Δd) in the Algonquin Highlands DMA, 1980-1997.

Variable	N	b (±se)	t	p	R^2	RMS
$d(t)$	228	-0.495 ±0.057	-8.72	<0.001	0.25	0.006
$d(t-1)$	210	-0.127 ±0.069	-1.84	0.067	0.02	0.008
$d(t-2)$	192	-0.147 ±0.074	-1.99	0.048	0.02	0.009
$d(t-3)$	174	-0.017 ±0.077	-0.22	0.82	0.00	0.009
$FD\text{-}H(t+1)$	209	-0.030 ±0.026	-1.15	0.25	0.01	0.008
$FD\text{-}C(t+1)$	157	0.065 ±0.045	1.44	0.15	0.01	0.008
$\overline{ED}(t+1)$	128	-0.006 ±0.014	-0.39	0.70	0.00	0.008
$LD(t+1)$	133	-0.065 ±0.064	-1.01	0.31	0.01	0.008
$\text{Log}_{10}\,\hat{A}(t)$	228	-0.023 ±0.009	-2.63	0.009	0.03	0.008
$\text{Log}_{10}\,\hat{K}(t)$	228	-0.032 ±0.014	-2.30	0.022	0.02	0.008
$\text{Log}_{10}\,\hat{B}(t)$	228	-0.030 ±0.017	-1.77	0.078	0.01	0.008
$T_P\,(t)$	227	0.001 ±0.004	0.14	0.88	0.00	0.008
$T_S(t)$	227	0.021 ±0.005	3.79	<0.001	0.06	0.008
$T_W(t)$	227	0.004 ±0.003	1.10	0.27	0.01	0.008
$R_P\,(t)$	227	$0.001 \pm 1\text{x}10^{-4}$	4.25	<0.001	0.07	0.008
$R_S\,(t)$	227	0.001 ±0.001	0.71	0.48	0.00	0.008
$Ws(t)$	228	$-1\text{x}10^{-4} \pm 3\text{x}10^{-4}$	-3.31	0.001	0.05	0.008

Table 4.2. Pearson correlation matrix for estimates of reproductive rates; fawn: doe rates from hunter surveys (FD-H) and check stations (FD-C); average number of embryos per doe killed ($\overline{ED}$); proportion of lactating does (LD), for all WMU and years in Algonquin Highlands, 1980-1997.

	FD-H	FD-B	ED	LD
FD-H	---			
FD-C	0.08	---		
ED	-0.08	-0.31	---	
LD	-0.21	0.23	-0.22	---

Table 4.3. Partial relationships of spring (T_P), summer (T_S), winter (T_W) temperature; spring (R_P), summer (R_S) rainfall; SDI (W_S) in year t, t-1, t-2 and t-3 and first-order interactions with d(t) and Δd(t→t+1), after accounting for effects d(t) and d(t-1) for AH, 1980-1997 (N =209).

Weather Variable	*Year*	*b (±SD)*	*t*	*p*	*R^2 (model)*	*RMS (model)*
T_P	t	-0.001 ±0.003	-0.32	0.75	0.27	0.006
	t-1	**-0.013 ± 0.004**	**-3.76**	**<0.001**	**0.32**	**0.006**
	t-2	-0.001 ±0.004	-0.34	0.73	0.28	0.006
	t-3	0.006 ± 0.004	1.46	0.15	0.28	0.006
T_S	**t**	**0.015 ±0.180**	**3.03**	**0.003**	**0.30**	**0.006**
	t-1	-0.008 ± 0.005	-1.45	0.15	0.28	0.006
	t-2	**-0.018 ± 0.005**	**-3.70**	**<0.001**	**0.32**	**0.006**
	t-3	-0.009 ± 0.005	-1.62	0.10	0.28	0.006
T_w	t	0.003 ±0.003	1.06	0.29	0.28	0.006
	t-1	-0.005 ±0.003	-1.63	0.10	0.28	0.006
	t-2	**-0.012 ± 0.003**	**-4.05**	**<0.001**	**0.33**	**0.006**
	t-3	0.004 ± 0.003	1.33	0.18	0.28	0.006
R_P	**t**	**5x10^{-4} ±1x10^{-4}**	**4.21**	**<0.001**	**0.33**	**0.006**
	t-1	5x10^{-5} ±1x10^{-4}	0.41	0.69	0.27	0.006
	t-2	-2x10^{-4} ±1x10^{-4}	-1.31	0.19	0.28	0.006
	t-3	1x10^{-4} ±1x10^{-4}	0.43	0.66	0.27	0.006
R_S	t	6x10^{-5} ±8x10^{-5}	0.68	0.50	0.27	0.006
	t-1	9x10^{-5} ±8x10^{-5}	1.07	0.28	0.27	0.006
	t-2	2x10^{-4} ±8x10^{-5}	1.85	0.07	0.29	0.006
	t-3	1x10^{-4} ±8x10^{-5}	1.34	0.18	0.27	0.006
W_S	**t**	**-5x10^{-5} ±3x10^{-5}**	**-2.14**	**0.03**	**0.29**	**0.006**
	t-1	-3x10^{-5} ±3x10^{-5}	-1.00	0.32	0.27	0.006
	t-2	**6x10^{-5} ±2x10^{-5}**	**2.29**	**0.02**	**0.29**	**0.006**
	t-3	4x10^{-5} ±2x10^{-5}	1.79	0.07	0.28	0.006
d(t)* T_P(t)		0.044 ±0.036	1.22	0.22	0.28	0.006
d(t)* T_S(t)		0.010 ± 0.054	0.19	0.85	0.27	0.006
d(t)* T_W(t)		0.010 ±0.036	0.28	0.78	0.27	0.006
d(t)* R_P(t)		0.002 ±0.001	1.12	0.26	0.27	0.006
d(t)* R_S(t)		0.002 ±0.001	1.68	0.09	0.28	0.006
d(t)*W_S(t)		-3x10^{-4} ±3x10^{-4}	1.13	0.26	0.28	0.006

Table 4.4. The best overall model to predict the change in our population index from year t to t + 1 $\Delta d(x,t \rightarrow t+1)$ for Algonquin Highlands, 1980-1997 (N =205, $R^2 = 0.46$).

Variable	*b (±s.e.)*	*t*	*P*
d(t)	-0.621 ±0.063	-9.77	<0.001
d(t-1)	0.290 ±0.065	4.48	<0.001
$\hat{A}$ (t) ($\log_{10}$)	-0.017 ±0.008	-2.05	0.04
Ws (t)	$-6 \times 10^{-5} \pm 3 \times 10^{-5}$	-2.21	0.03
Ws (t-3)	$6 \times 10^{-5} \pm 2 \times 10^{-5}$	2.57	0.01
T_P (t-1)	-0.014 ±0.003	-4.52	<0.001
T_S (t)	0.017 ±0.005	3.37	<0.001
T_S (t-2)	-0.023 ±0.004	-5.02	<0.001

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Figure 4.2. Change in our population index (d) from year t to t+1 ($\Delta d(t,t+1)$) versus the population index in year t ($d(t)$) for all WMU and years in Algonquin Highlands, 1980-1997

Figure 4.3. Standardized partial coefficients (b') for factors in the best model to predict change in an index of population (Δd) from year t to t+1, for all WMU and years in the Algonquin Highlands, 1980-1997. Factors included in the model were population index (d) in year t and t-1, antlerless kill (A) in t, snow depth index (Ws) in t and t-3, average spring temperature (T_P) in t-1 and average summer temperature (T_S) in t and t-2.

Figure 4.4. Predicted versus observed change in population index (d) from year t to t+1 from the best model shown in Table 4.4.

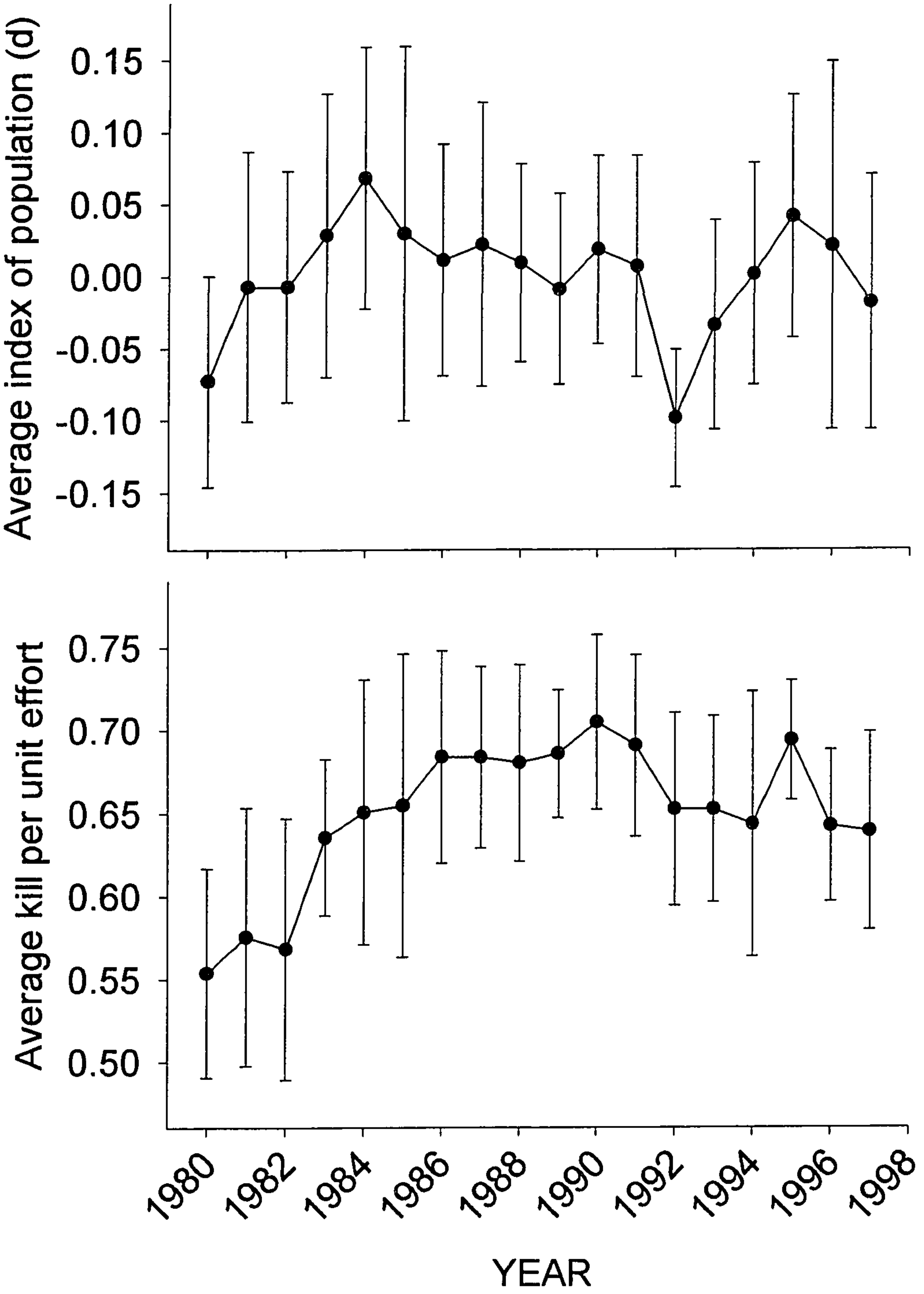

Figure 4.1. Yearly mean (± standardard error) population index (d) and kill per unit effort (KPUE) for all WMU in AH, 1980-1997.

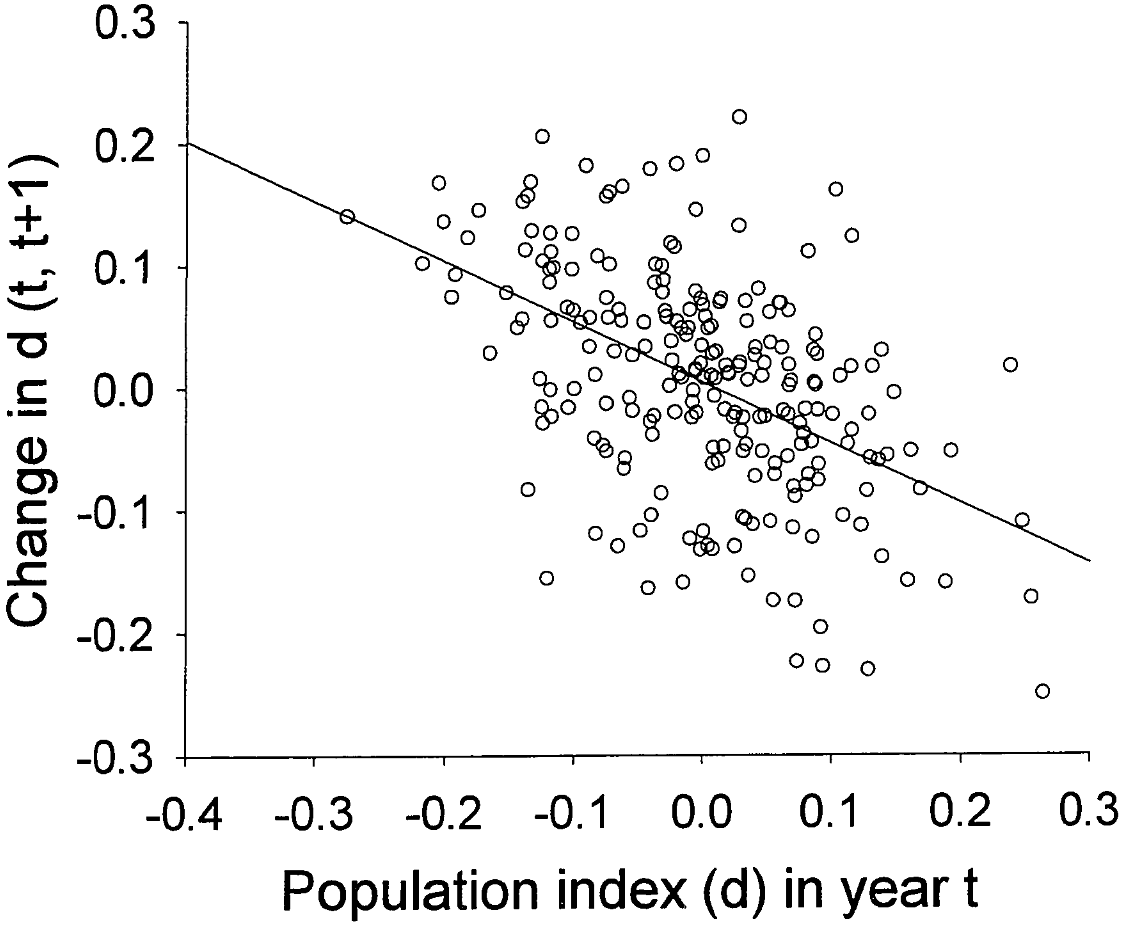

Figure 4.2. Change in our population index (d) from year t to t+1 (Δd(t,t+1)) versus the population index in year t (d(t)) for all WMU and years in Algonquin Highlands, 1980-1997

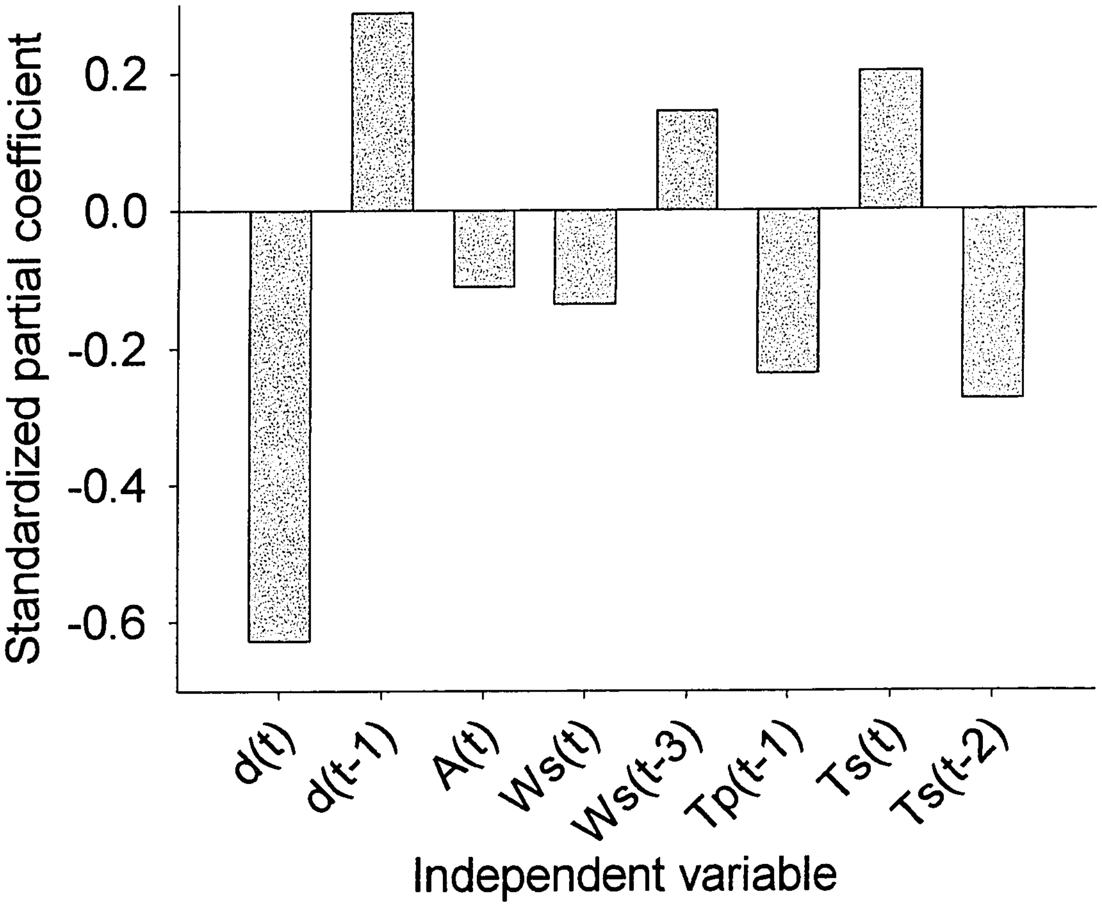

Figure 4.3. Standardized partial coefficients (b′) for factors in the best model to predict change in an index of population (Δd) from year t to t+1, for all WMU and years in the Algonquin Highlands, 1980-1997. Factors included in the model were population index (d) in year t and t-1, antlerless kill (A) in t, snow depth index (Ws) in t and t-3, average spring temperature (T_P) in t-1 and average summer temperature (T_S) in t and t-2.

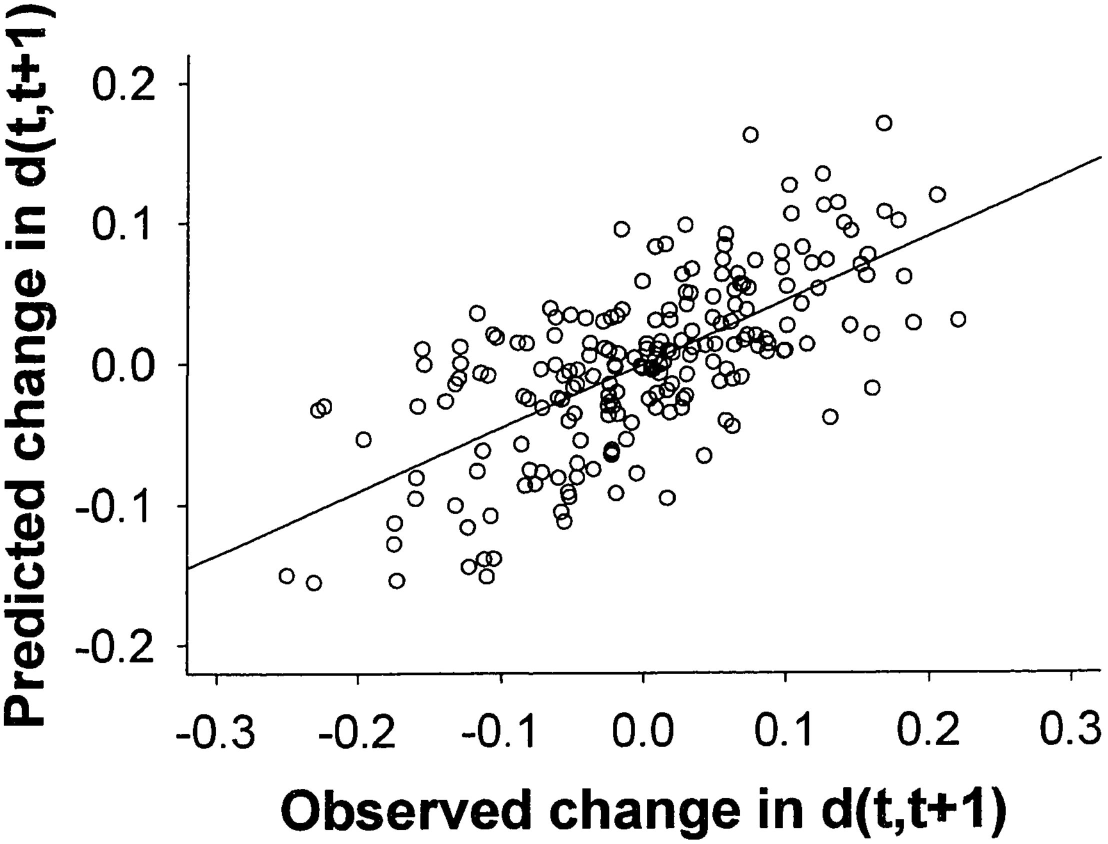

Figure 4.4. Predicted versus observed change in population index (d) from year t to t+1 from the best model shown in Table 4.4.

Chapter 5: Geographical variation across Ontario in (inferred) white-tailed deer population dynamics.

Introduction

The Ontario Ministry of Natural Resources is responsible for white-tailed deer management throughout Ontario, and, as such, is involved with data collection and analysis at the level of individual wildlife management units throughout the province. From the regulatory perspective, an important issue is the extent to which management models developed (and implemented) in one part of the province can be applied to other regions. High model generality (which means, in practical terms, that a model developed for one region can be applied to another with little loss of predictive power) implies that the major elements of a deer management strategy can be developed at large geographical scales and simply implemented at smaller scales, thereby achieving some savings associated with the economies of scale. On the other hand, low model generality implies that in order to obtain some specified level of predictive power, management strategies may need to be developed for individual geographical units.

Second, to be effective any deer management strategy must be based on an understanding of the true (as opposed to assumed) causal factors underlying deer population dynamics. A crucial element in "evidence-based" deer management then is the weight of evidence associated with any putative causal factor. This weight of evidence is, at least in part, related to the number of experiments in which the factor in question is implicated: if a number of independent experiments consistently point to the same causal factor, then we are less likely to be deluding ourselves that the factor in question is in fact important. In epidemiological research, weight of evidence is often based on spatial or geographical replication: if, in a number of different geographical settings, Y is consistently correlated with (putative) causal factor X, this is viewed as stronger evidence of a (true) causal link between X and Y than if such a correlation is detected only sporadically.

In Ch. 4, we evaluated specific hypotheses about (putative) causal factors by deriving a statistical model that predicts annual changes in an index of white-tailed deer density for the Algonquin Highlands deer management area (DMA). This model supports the hypothesis that in the Algonquin Highlands DMA, white-tailed deer population dynamics are density-dependent. Moreover, our results suggest that in this area at least, both antlerless kill and weather effects have historically had only small impacts on population dynamics. In this chapter, we expand our analysis to different DMAs to see if the same results are obtained.

Methods

The province is divided into 8 Deer Management Areas (DMA) based on similar climate, and physical characteristics: Lake of Woods (LOW), Thunder Bay (TB), Sudbury (SUD), Algonquin Highlands (AH), Eastern Midlands (EM) and Manitoulian Island (MAN), Central Agriculture (CA) and Southern Agriculture (SA) (see map in Appendix I), each including one or more wildlife management units. For some DMAs, historically low hunter numbers in individual WMUs resulted in few returned surveys for the Provincial Mail Survey. To remove potential errors in harvest reporting due to small survey numbers (sample size), only WMU and years with at least 20 surveys returned were included in the analysis. This exclusion of entire WMUs from the analysis means that for some DMAs with low deer hunter numbers (e.g. TB and SUD), overall sample sizes are relatively small.

Our index of population density was deer seen controlling for effort, calculated by taking the residuals (*d*) from the linear regression of log 10 deer seen versus log 10 effort for all WMU and years combined. The change in population (Δd) from year t to $t+1$ within a WMU (x) was calculated as;

$$\Delta d(x)t \rightarrow t+1 = d(x, t+1) - d(x, t) \qquad (1)$$

Type 1 linear regression was used to determine the relationship, for non-AH WMU, between Δd and deer density(d) in years t and t-1, the estimated log10 antlerless harvest ($\hat{A}$)and weather data in year t. Weather data were obtained from the Canadian Daily Climate, Eastern Canada 1998 CD-ROM published by the Climate Products and Publishing Division, Climate and Water Systems Branch, Environment Canada, as previously described. Daily total precipitation and average temperature data were used to calculate the following variables for each WMU (x) and year (t);

a) $R_P(x,t)$ ≡ total rainfall from April to May (spring)

b) $R_S(x,t)$ ≡ total rainfall from June to August (summer)

c) $T_P(x,t)$ ≡ average daily temperature, April – May (spring)

d) $T_S(x,t)$ ≡ average daily temperature, June – August (summer)

e) $T_W(x,t)$ ≡ average daily temperature, November – March (winter)

The Snow Network for Ontario Wildlife (SNOW) provided another measure of winter severity (Ws), the snow depth index (SDI) calculated as the cumulative snow depth for the entire winter (cm), measured at a series of stations across the province. For each WMU (x) and harvest year (t), *Ws* was taken from the most representative station or average of multiple stations as designated by the OMNR (Warren et al., 1998).

We did not investigate potential lag effects of weather, though our analysis for the AH DMA showed statistically significant relationships between Δd and the snow depth index, summer and spring temperature in years t-1, t-2…etc. However, these variables explained only a small amount of additional variance in Δd and hence are excluded here for simplicity.

In order to investigate the applicability of an overall provincial model, we tested for significant interactions between each significant predictor and DMA (a categorical variable), which would indicate inter-DMA difference in regulatory effects.

While DMA groupings are based on similar climatic and geological conditions, differences between WMU in the factors that regulate population, beyond those accounted for by DMA, may obscure their true effects. Unfortunately, small sample sizes preclude an effective analysis of between WMU differences. Therefore cluster analysis was used to produce groupings of WMU, independent of DMA, in an attempt to better represent differences between WMU in the factors that regulate population and thereby improve model fit and usefulness.

A variety of clustering methods, using different combinations of factors, were attempted with most failing to produce identifiable WMU groups and/or better population models. Accordingly, we have chosen to focus on 3 factors; population index (d), antlerless kill ($\hat{A}$) and snow depth index (Ws), due to their demonstrated (for population density) or assumed (for kill and snow) importance in population regulation. Specifically, in addition to potentially providing better population models, this cluster attempt may reveal differences between WMU or interactions that are obscuring kill and SDI effects

Hierarchical Cluster Analysis, using complete linkage (farthest-neighbour) of euclidian distances was used to regroup WMU based on their mean and maximum (all values standardized to the mean and standard deviation) population density (d), snow depth index (Ws), and estimated total antlerless kill ($\hat{A}$). Maximum values were included in recognition of possible threshold effects of snow and antlerless kill, which may result in the mean values being less indicative of the true effect of these values.

Linear models to predict Δd were then created for these groups to determine if they provided different or better models than those based on DMA groupings.

Results

Regulatory factors for non-AH data

For the pooled (over DMA) data there was a significant negative bivariate relationship between Δd and $d(t)$ (b= -0.345 ± 0.032, t = -10.7, p <0.001, R^2 =0.17, RMS = 0.017) (Fig. 5.1). The previous year's population density, $d(t-1)$ had a significant positive effect above and beyond the effect of $d(t)$ (b= 0.384±0.048, t = 7.90, p < 0.001) that both improved model fit (R^2 =0.25, RMS = 0.016) and increased the effect size for $d(x,t)$ (b = -0.604±0.048, t = -12.5, p <0.001). Accounting for differences between DMA in mean Δd (F = 2.72, df = 6, p =0.013), and marginal differences in the effects of $d(t)$ and $d(t-1)$ between DMA ($d(t)$*DMA: F = 1.87, df = 6, p = 0.08; $d(t-1)$*DMA: F = 2.56, df = 6, p = 0.01) improved model fit (R^2 = 0.31, RMS = 0.015).

While antlerless kill showed a statistically significant negative bivariate relationship with Δd (b=-0.036±0.012, t=-2.98, df=541, $p< 0.001$) it explained little variation (R^2 =0.02, RMS = 0.019) and was not statistically significant after accounting for the effects of $d(t)$ and $d(t-1)$(b = 0.006±0.014, t=0.437, df = 474, p = 0.66). Additionally, there was no significant difference between DMA in the relationship between antlerless kill and Δd ($\hat{A}$ (t)*DMA: F = 0.99, df = 6, p = 0.42).

The only significant bivariate relationships observed between Δd and weather variables were a negative effect of snow depth ($b = -1.0\text{x}10^{-4} \pm 3\text{x}10^{-4}$, t = -6.46, $p <$ 0.001, R^2 = 0.07, RMS = 0.018), and a positive effect of summer temperature (b = 0.018±0.004, t = 4.21, p = 0.001, R^2 = 0.03, RMS = 0.020).

Using stepwise linear regression, the best multiple model to predict Δd included $d(t)$, $d(t-1)$, Ts, Ws and Tp (N=448, R^2 =0.35, RMS = 0.013), though the individual contributions of all factors, compared to d(t) were relatively small (Fig. 5.2). After accounting for weather, there was no significant difference between DMA in mean Δd (F = 1.25, df = 6, p = 0.27) nor any significant difference between DMA in the effect of any independent variable (All DMA*variable interactions, p > 0.10).

When data from AH were included, there were significant differences between DMA in the effects of $\hat{A}(t)$ (F = 3.66, df = 7, p <0.001), $d(t)$ (F = 3.59, df = 7, p < 0.001) and $Ws(t)$ (F = 2.37, df = 7, p = 0.021), though it only moderately improved model fit (RMS = 0.010 vs. RMS (w/o interactions) = 0.011).

Cluster analysis

Hierarchical cluster analysis on the mean and maximum of *d*, *Ws* and $\widehat{A}$ for each WMU (standardized to units of standard deviation from the provincial mean) yielded 7 groups and one outlier, WMU 39 which had only 2 years of data (Fig. 5.3). The distribution of groups compared to DMA is shown in figure 4. Mean(± s.d.) and maximum values of *d*, *Ws* and $\widehat{A}$ (± s.d.) are shown for each group (Table 5.1).

The best model obtained to predict Δd from the previous analysis, plus antlerless kill, was fit along with group as a categorical variable and the interactions between each independent variable and group. While there was no difference in mean Δd (F=0.78, df = 6, p = 0.58), there were statistically significant differences in the effects of $d(t)$ (F= 2.15, p = 0.04), $\widehat{A}(t)$ (F=3.67, p = 0.001) and $Ws(t)$ (F = 2.38, p = 0.03) between groups, which accounted for only a small amount of variance beyond that explained by DMA (RMS = 0.009 vs. RMS = 0.010).

Differences in population regulatory effects were assessed by comparing the standardized coefficients (b') for each group (Fig. 5.5). For all groups $d(t)$ had the strongest (negative) effect on Δd, consistent with previous models, while $d(t-1)$ had a consistent positive effect, though it was not always statistically significant. Standardized coefficients were larger for those groups with larger (population) mean population index (1, 2A, 2B, 4) compared to those with smaller (negative) values.

$\widehat{A}(t)$ exhibited a relatively strong negative effect on Δd in 3B, which had the second highest mean kill and relatively small mean population. Additionally, there were marginal negative effects for group 1, which had the highest mean kill, and 2C where both mean kill and mean population were relatively low. Antlerless kill was not significant (and often positive) in the remaining groups.

Ws had significant negative effects in 3 groups (3a, 3b, 4), which consisted of northern WMU. The standardized coefficients for Ws were negatively related to mean Ws for the group (Fig 5.6). Spring temperature conversely, showed significant negative effects in groups containing southern WMU (1, 2A, 2B, 2C) and was not significant in groups with significant Ws effect (3A, 3B, 4). Summer temperature had consistent positive effect on change in the population index for all groups.

Discussion

The results from the other DMA corroborate the main finding from our analysis of population regulation in the Algonquin Highlands data, namely, a negative relationship between change in deer density from year t to t+1 and the density in year t, the classic signal of density-dependence. In addition, there were similar, limited effects of summer temperature, spring temperature and snow depth. Antlerless kill, however, showed even less of a historical regulatory effect outside of the Algonquin Highlands

On a provincial scale there was relatively high model generality; in terms of similar main effects, population density in t and t-1 and summer temperature, little evidence of a significant regulatory effect of harvest, and poor model fit across DMA and WMU groups from the cluster analysis. The small differences between both DMA and cluster analysis groupings in the effects of some factors, SDI, spring temperature and kill, had little effect on model predictive ability, though may provide some useful insight into the management of deer populations

A statistically significant (negative) effect of antlerless kill was detected only for a few WMUs with comparatively high historical kills, and relatively low historical population densities, most of which are located in the heavily hunted Algonquin Highlands. For most WMUs in the province, the level of antlerless kill experienced from 1980-1997 had no observable effect on the number of deer seen per unit effort, our index of population. These results suggest that in order for antlerless kill to have a significant regulatory effect, a significant portion of the population must be removed. The historical lack of an effect of kill does not preclude future harvest from affecting population, if the levels of kill and/or population density change.

The impacts of weather on population change, while still small compared to the magnitude of the density-dependent effect, varied from north to south. Snow depth had an observable negative effect on populations that declined with mean snow depth and was not evident in southern WMUs. Conversely, a negative relationship with spring temperature evident in the south was not observed in the north.

Deep snow and warm springs may affect deer populations in a similar manner by lowering doe condition in the spring when fawns are born, resulting in higher post-natal fawn mortality and lower recruitment (Verme 1977, Langvatn et al. 1996). In northern WMUs the spring effect may be less important than in-utero and post-natal loss of fawns (Verme 1977) and/or direct winter mortality from starvation and predation (Nelson and Mech 1986, Dumont et al. 2000, Lamoreux et al. 2001) from the more severe winters experienced. Mild southern winters may result in less direct winter mortality but still result in poor doe physical condition, thereby increasing the importance of spring conditions for doe recovery prior to giving birth and fawn survival. There may be other negative effects of warm springs in southern WMU that have not been studied (e.g. increased disease or parasites).

Summer temperature exhibited the strongest and most consistent weather effect on population change regardless of deer density, kill or snow depth. Presumably, good summers allow for better fawn survival and recruitment rather than relating to direct adult mortality. Little attention has been paid to the role of summer conditions for deer in Ontario, as winter conditions were assumed to be the limiting factor (Voigt et al. 1992) and there are few significant effects documented in the literature (Langtavn et al. 1996).

While not greatly improving our population models, these empirical patterns may provide some guidance for managers. A comparison of WMU with and without a kill effect, may provide a rough estimate of the level of future harvest, in relation to population, that would be needed to down-regulate population or at least indicate those WMU where kill is likely to have no effect. The north-south gradient in the effect of snow depth suggests a potential threshold relationship not being accurately modeled or captured with the data collected. A potential greater importance of spring and summer conditions, especially in southern WMU, may also require consideration and further study.

Data from other DMA provided further evidence for the main findings from the Algonquin Highlands; deer populations are regulated by factors beyond management control, density dependence and weather, and historically kill had limited use as a regulatory tool. There would appear to be little gain from developing population models at a finer geographical scale (above the WMU level), as opposed to using a provincial model. Though this finding reflects the poor quality of all models more than generality of the provincial model, as those factors that do vary across the province (SDI, spring temperature, kill) have minor effects at best. The predictive ability of the provincial model, while likely to be poor, is assessed in the following chapter.

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Table 5.1. Mean (±sd) and maximum values of population index (*d*), snow depth index (cm) (*Ws*) and estimated antlerless kill ($\hat{A}$) for groups of WMU as determined by cluster analysis, 1980-1997.

Group	N	d(t)		Ws(t)		$\hat{A}(t)$	
		Mean(±sd)	Max.	Mean(±sd)	Max.	Mean(±sd)	Max.
1	58	0.06±0.16	0.47	566±215	1249	1316±794	3156
2a	114	0.13±0.14	0.43	435±202	831	399±321	1558
2b	125	0.07±0.13	0.43	541±183	988	207±136	614
2c	70	-0.11±0.13	0.25	322±144	722	176±172	790
3a	90	-0.19±0.12	0.08	673±254	1353	159±165	823
3b	122	-0.07±0.10	0.17	616±203	1137	585±420	1849
4	49	0.11±0.19	0.65	686±293	1447	181±181	902

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Figure 5.6. Relationship between the standardized partial regression coefficient (b′) for snow depth index, from the model to predict change in an index of population density (Δd) for each WMU grouping and the group mean snow depth index ($\overline{Ws}$).

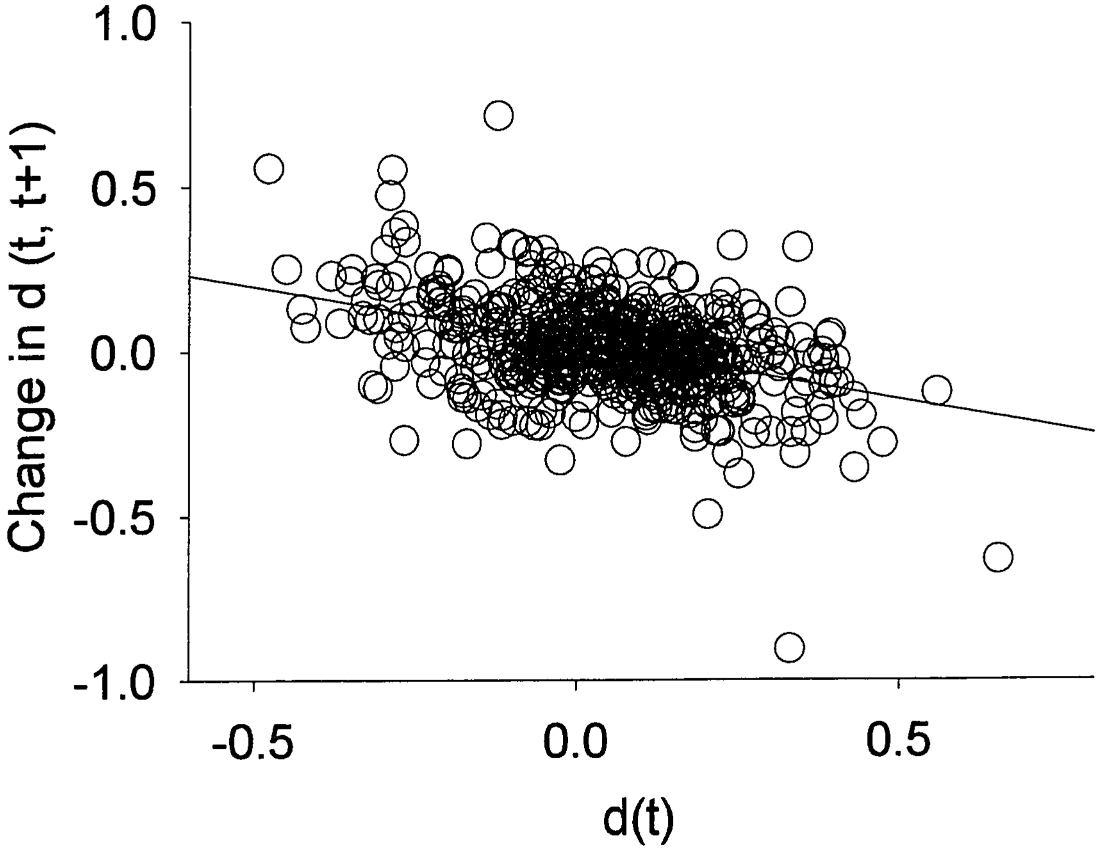

Figure 5.1. Change (Δ) in the population index (d) from year t to t+1 in relation to the population index in year t, for all WMUs in Ontario outside of the Algonquin Highlands DMA, 1980-1997.

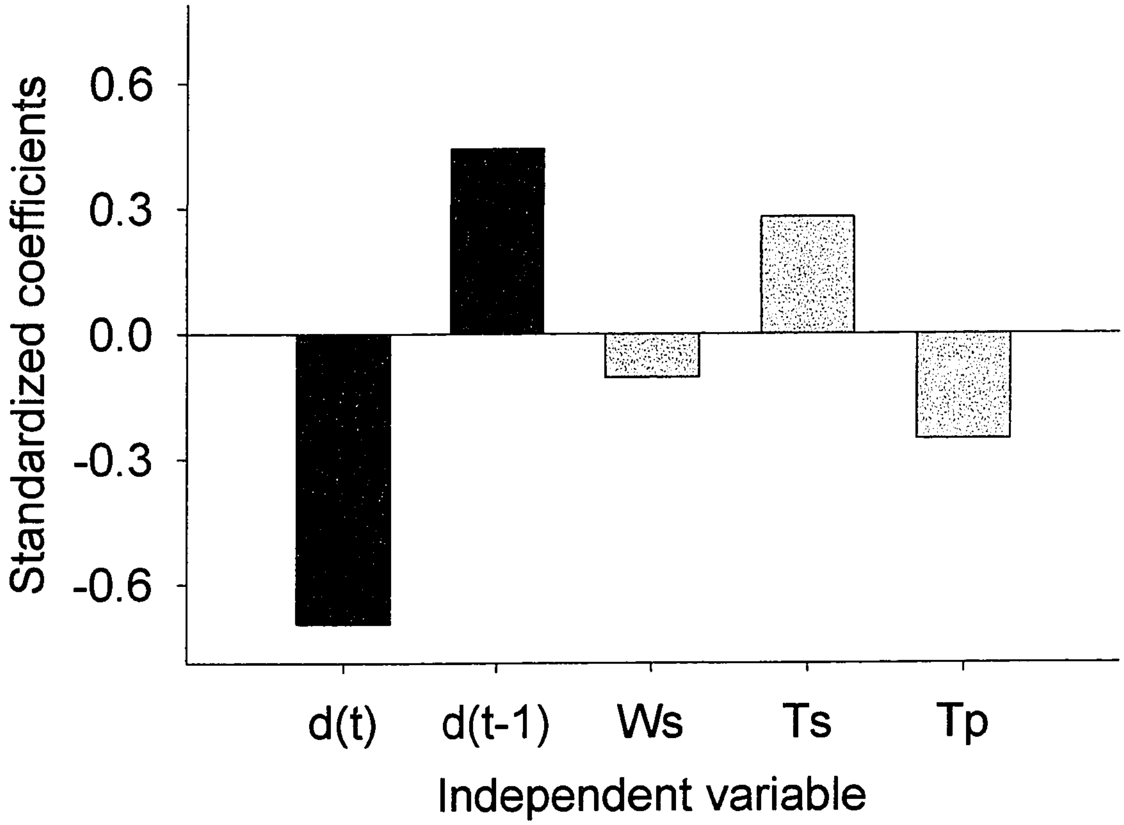

Figure 5.2. Standardized partial regression coefficients from the best model predicting change in an index of population density ($\Delta d(t,t+1)$) from the index of population density(d) in year t and t-1, snow depth index (Ws), and spring (T_P) and summer (T_S) temperature (all in year t) for WMU outside of the Algonquin Highlands, 1980-1997.

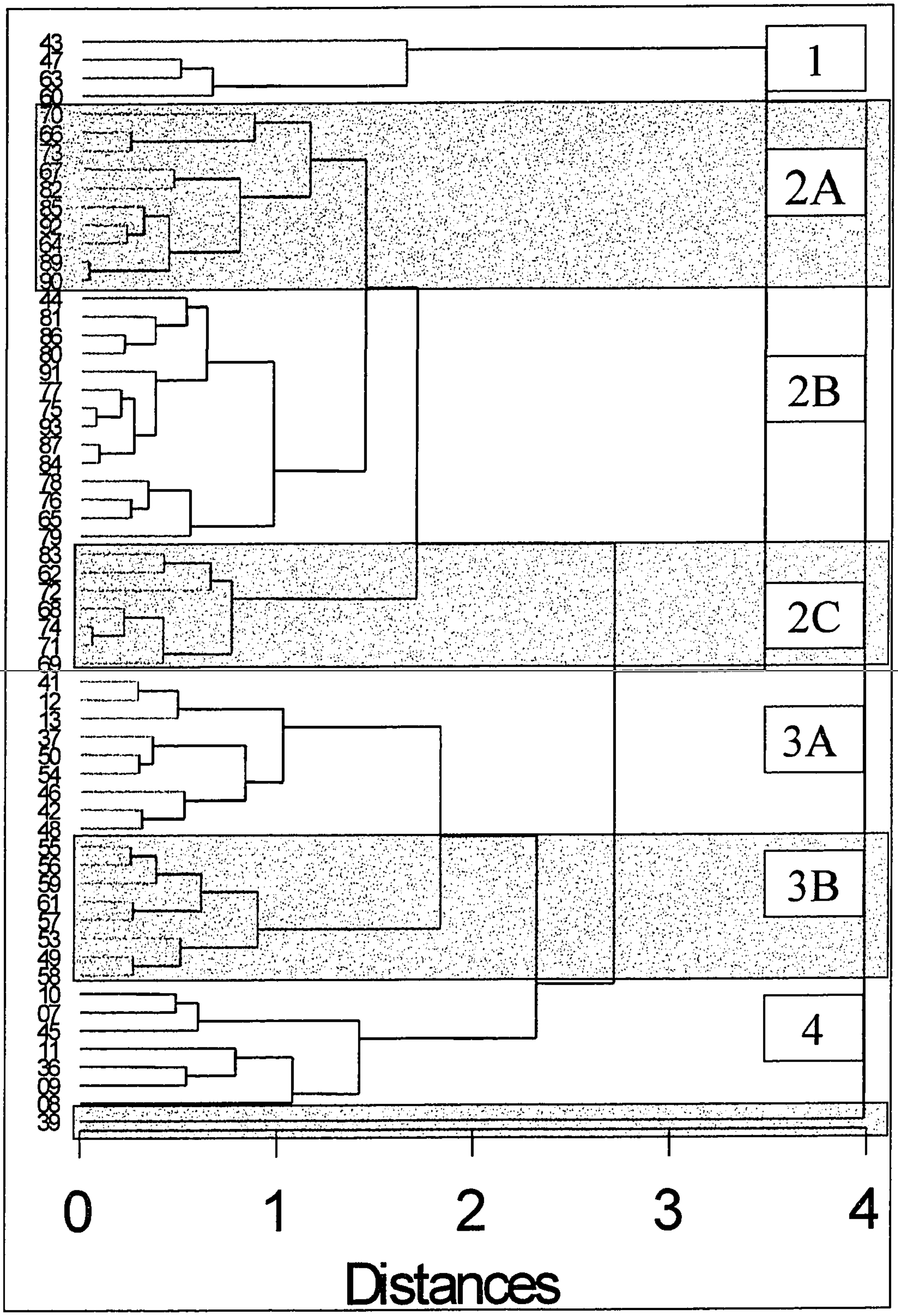

Figure 5..3. WMU groupings obtained from hierarchical cluster analysis based on the furthest-neighbour clustering of euclidian distances of the minimum, maximum and mean population index (d), antlerless kill and SDI, standardized to units of standard deviation from the overall mean.

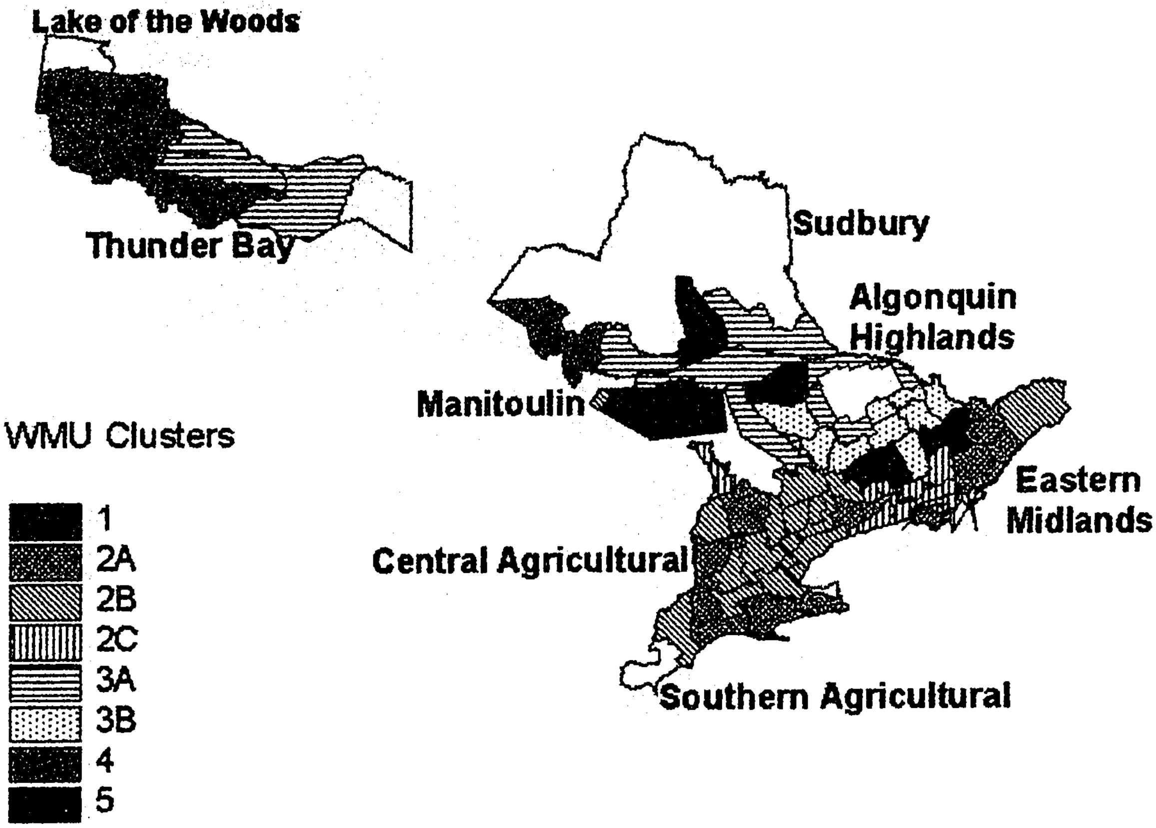

Figure 5.4. Map showing the geographical distribution of WMU groupings obtained from a hierarchical cluster analysis of the standardized WMU means for index of population density (d), antlerless kill ($\hat{A}$) and snow depth index (W_S).

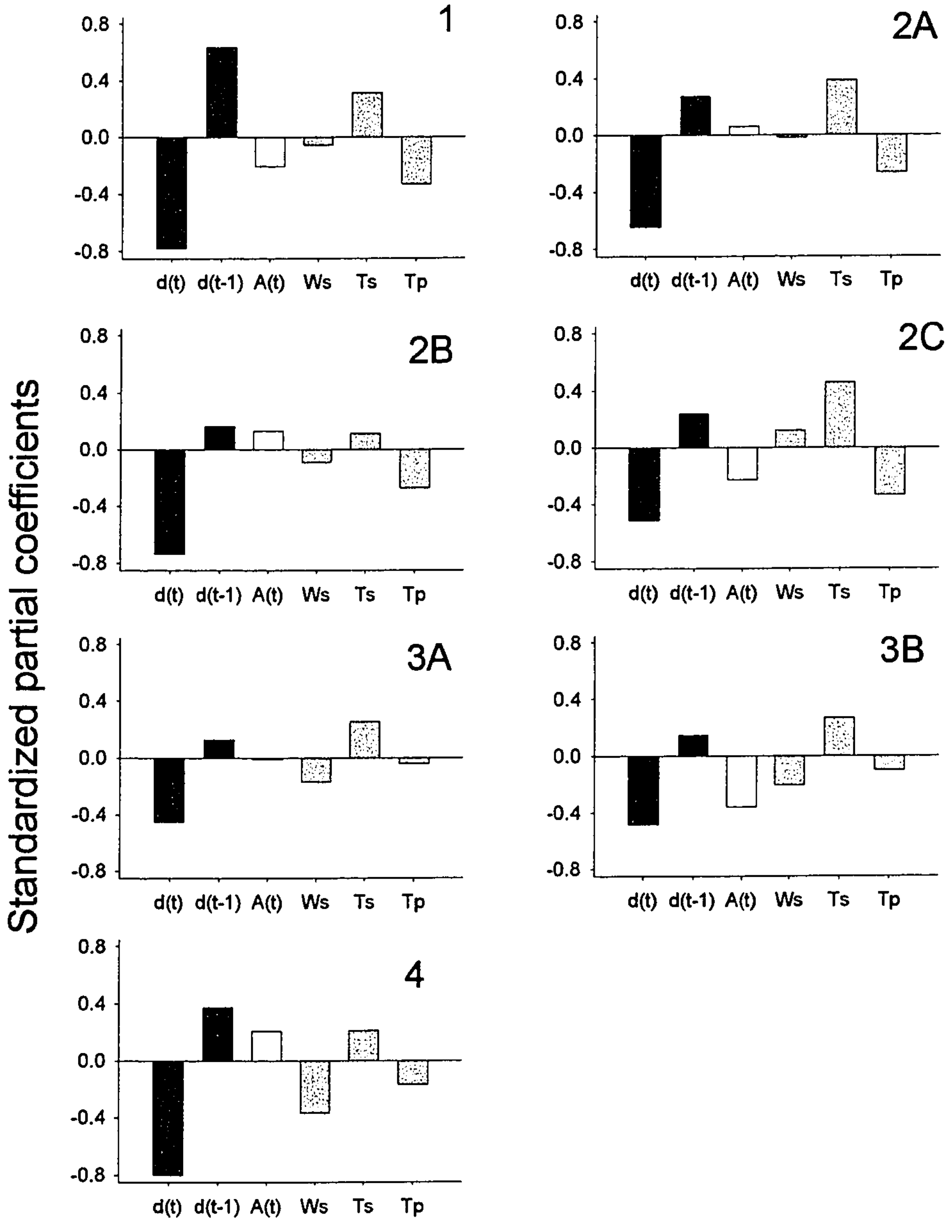

Figure 5.5. Standardized partial regression coefficients from models to predict the change in an index of population density (Δd) from year t to t+1, from the index of population density (d) in year t and t-1, snow depth index in year t (Ws), and spring (T_P) and summer (T_S) temperature; by WMU groupings shown in figure 4.

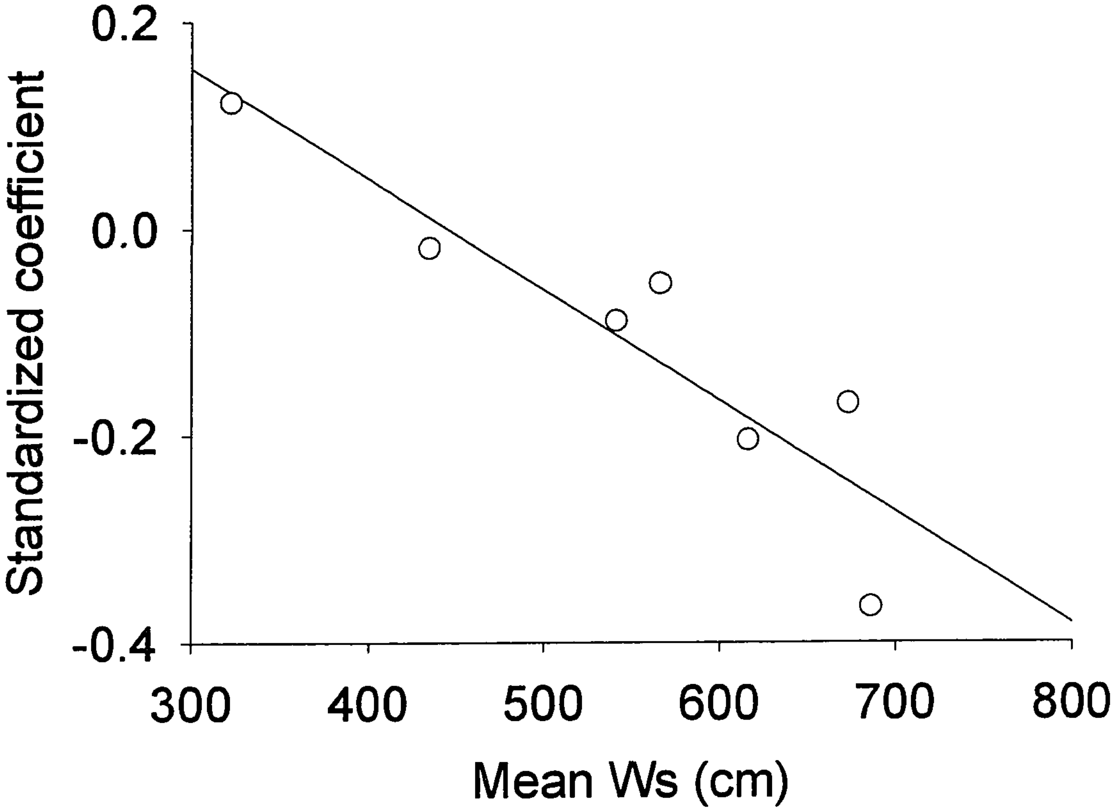

Figure 5.6. Relationship between the standardized partial regression coefficient (b′) for snow depth index, from the model to predict change in an index of population density (Δd) for each WMU grouping and the group mean snow depth index ($\overline{Ws}$).

Chapter 6: Model predictive power and management implications

Introduction

In previous chapters, we constructed statistical models relating changes in an index of population density (deer seen corrected for effort) between years t and t + 1 to population density, antlerless kill and various weather factors in year t and previous years, for a number of different geographical areas in Ontario. This exercise allowed us not only to test various hypotheses concerning the factors affecting deer population dynamics, but also to assess the historical impacts of regulatory factors (e.g. antlerless kill) on population dynamics. In principle, such an exercise could provide a simple model that would allow deer managers to accurately forecast future (i.e. next year) deer population densities, and hence regulate harvest to achieve a desired population level.

In practice, however, the models derived in our previous analyses have three practical limitations. First, a model that predicts annual changes in deer density (and hence, deer densities one year into the future, i.e. at time t + 1) is not very useful for management because decisions on harvest must be made before the data required to make the prediction are in hand. That is, if we desire a certain level of population index d in the fall of year t +1, the models constructed thus far include only those variables measuring characteristics of the system during the fall and winter of year t (e.g., harvest in year t, snow depth, etc.) and the spring/summer of year t + 1 (e.g. spring and summer temperature). These data are unavailable when decisions about the harvest in year t have to be made (i.e. late summer/early fall of year t). Hence, for management purposes, a model that predicts 2 years in the future is required, so managers may alter the intervening harvest (i.e. at t + 1), to achieve the desired target population in year t + 2.

Second, managers make management decisions (e.g. set tags) based on certain expectations of the effect of such decisions, within a given geographical unit (WMU) over a short time span, (usually, the impact on the harvestable population in the next couple of years at most). So, what matters to a manager is the answer to the following question: If I make a management decision now, what is the likelihood that the expected effect of this decision over the next year or two will in fact come to pass? Thus, what matters is not just the expected outcome of a management decision based on some model, but the distribution of possible outcomes associated with a single decision. The modeling exercise so far provides only a predicted outcome, but does not address the likelihood of this predicted value being correct, (i.e. the predictive power).

Third, our population density index is based on the residuals (*d*) of the regression of log 10 deer seen on log10 hunter effort, that is, the difference between the predicted number of deer seen ($\hat{S}_i$) based on effort and the actual number of deer seen (S_i). This index differs from the more standard index of density, harvest (or sightings) per unit effort, much more widely used in wildlife management circles. Thus, the practical value of the models would be enhanced by a change in the dependent variable, from the change in d between t and t + 1, to the change in deer seen per unit effort (ΔDE).

Methods

We first found a linear transformation between *d* and *DE* and calculated the change in deer seen per unit effort (ΔDE) from year t to t+2 as

$$\Delta DE = \log 10\, DE_{t+2} - \log 10\, DE_t \qquad (6.1)$$

Type I linear regression was then used to determine the effects of $DE\ t$, $DE\ t\text{-}1$, log 10 antlerless kill ($\hat{A}$), snow depth index (W_S), average summer (T_S) and spring (T_P) temperature on ΔDE for each of the WMU(x) and year (t) for the 7 groups of WMU previously identified by cluster analysis on WMU mean and max population index (d), antlerless kill ($\hat{A}$) and snow depth index (W_S)(see Ch. 5). The predictive power of the best model, i.e. the model with the lowest *RMS*, was then evaluated as described below.

Assessing predictive power

To assess predictive power, a jackknifed cross-validation approach was used. For each trial, one of n data points was excluded, and the model fitted to the remaining n -1 data points. The fitted model was then used to predict the value ($\hat{\Delta} DE$) of the single excluded datum. This procedure was repeated n times, resulting in n jackknifed observed-predicted pairs. Each observed and predicted ΔDE was transformed to a percentage change $\Delta DE(\%)$ from the absolute value of the observed DE (log values were all negative) in year t

$$\Delta DE(\%) = (\Delta DE / \text{abs}(\log 10\ DE_t)) * 100 \qquad (6.2)$$

$$\hat{\Delta} DE(\%) = (\hat{\Delta} DE / \text{abs}(\log 10\ DE_t)) * 100 \qquad (6.3)$$

With respect to predictive power, the key issue is the probability that the model will, for a given jackknifed datum, provide a prediction within X% of the observed value. To this end, error ranges or "bins" were created with a specified width of $\Delta DE(\%)$, starting with a bin 0 centered around 0 and extending in both positive and negative directions. For example, for a bin width = 20%, bin 0 extends from -10 to 10%, bin 1 from 10 to 30%, bin –1 from -10 to –30%. For each jackknifed trail, the observed and predicted ΔDE were assigned to the appropriate bin, and over all jackknifed trials the number of times the observed and expected values fell into the same bin was recorded. An accurate prediction (i.e. a prediction accurate to the (quantum) error defined by the bin width) is one in which both observed and predicted values fall into the same bin. This process was repeated for a range of bin widths (quantum errors). The result is, for a given bin width, an estimate of the predictive power of the model. For example, if bin width = 20% and 80% of the jackknifed observed-expected pairs fall into the same bin, we conclude that the actual change in deer seen per unit effort has a probability of 0.80 of being within +/- 10% of the predicted value.

We can consider bin width a measure of empirical uncertainty associated with the measurement of population density at the WMU scale. More specifically, it quantifies measurement error: a large bin width means that two different estimates of population density (e.g. for two different years) must be very different numerically before we are reasonably confident that they represent real differences. By contrast, a narrow bin width implies low measurement error, so that even though two estimates may be quite similar numerically, we are confident that they represent real differences.

From the above description it is clear that the wider the bins, i.e. the larger the measurement error, the greater the likelihood that both members of an observed-expected pair will fall into the same bin, i.e. the greater the assessed predictive power. Thus, to get an upper bound on predictive power, we selected a very coarse bin resolution and in fact define only three bins corresponding to no change, density increase and density decrease. The latter two bins have no upper and lower bounds respectively, so that their widths are controlled only by the width of the no change bin centred at zero (fig. 6.1).

As noted above, bin width is determined by measurement error. Thus, an observed change in population would be classified as no change (i.e. would fall into the center bin) if its absolute magnitude were less than the measurement error. As we have (unfortunately) no measure of the sampling error in *DE*, we assumed that sampling error within a WMU must be less than or equal to the observed variation in *DE* between years, as presumably some of the observed variation in *DE* over time within a WMU reflects real changes in population density. The standard deviation of *DE* for each WMU (over time) was determined and the average value over all WMUs was calculated ($\overline{sd} = 0.08$). Based on the average *DE* for the province as a whole this corresponds to approximately 19.6% change in population. We therefore used bin widths of +/- 0, 1, 2, 3, 4, 5, 7.5, 10, 12.5, 15,17.5, and 20% for the middle (no change bin).

For the 3-bin situation, overall accuracy (which would include the ability to predict no change) will decrease as the 3rd bin is expanded, reflecting the change in resolution from 2 to 3 bins. Eventually, at some point, the no change bin will expand to contain most data points and accuracy will increase, eventually reaching 100% (i.e. all observed and predicted values fall into one bin). Therefore, it is more informative to assess the model's ability to predict changes in population (i.e. those values that are above or below the no change limits), which can be measured in 2 ways. Model accuracy, is the likelihood that a predicted changes (increase or decrease) is correct, calculated as;

Accuracy = Correct Predicted Changes / Total Predicted Changes

Alternately, model sensitivity is the likelihood that an observed population change (increase or decrease) is captured by our model, calculated as;

Sensitivity = Correctly Predicted Changes / Total Observed Changes

Increasing no change bin width may have different effects on model accuracy versus sensitivity (i.e. a model may become more accurate but less sensitive or vice versa). Deciding which aspect of the model is more important depends on which is viewed as more costly, falsely predicting a population change that does not occur (poor accuracy) or failing to predict an actual population change (poor sensitivity).

Results

Over all WMUs and years, log 10 *DE* showed a strong linear relationship with d (Fig. 6.2). Model fits, as indicated by *RMS*, for ΔDE for a two year period, i.e. between t and t + 2, were consistently lower than for a single year (t, t+1) (Table 6.1). The best model fit was obtained for group 3B, a group of northern WMU with an observable regulatory effect of antlerless kill (Table 6.1), and was the model chosen to explore predictive power using the bin method described above.

The distribution of ΔDE(%), for both observed and predicted changes, was relatively normally distributed around 0, though with a slightly longer negative tail (Fig. 6.3). The majority of data points were between ± 25%, though the observed changes had a higher proportion of values beyond ± 25%.

For the finer resolution model, which employed a constant bin width (centered at 0), as bin width was increased the proportion of observed and expected pairs that fell into the same bin increased, though overall accuracy was poor (Fig. 6.4). At a resolution of ± 10% the model had an accuracy of 36% (42/116), meaning that for any predicted value we would have a 36% chance of being with +/-10% of the actual value. At the coarser resolution of ±20%, model accuracy, while nearly double, was still only 60% (70/116), an especially poor result considering the large bin width results in most values "falling" into the central bin (i.e. <20% population change in most years). In comparison, for 1000 random pairs of the observed and predicted values, the mean accuracy rate was 47± 3% (95%CI: 41-53%). So our model was only 13% more accurate than randomly picking a number.

In an attempt to improve model accuracy, a more coarse resolution was applied, where all values greater than (less than) the upper (lower) boundaries of the no-change bin occupy the same bin (decrease or increase respectively). For a no-change bin width of zero, there are only two bins, increase or decrease, making this the coarsest resolution. At this resolution the predicted value was correct 76% of the time (i.e. 24% of the time the model predicted the wrong direction of change from year t to t+2), with little difference in the accuracy of predicting increases (75) versus decreases (77).

Increasing the resolution of our model, by differentiating changes less than sampling variation from "real" population changes, introduced a 3rd bin (the no-change bin). Increasing the width of this 3rd bin had little effect on model accuracy in predicting decreases, but resulted in lower accuracy for predicted increases (Fig. 6.5). Model sensitivity, was consistently higher for decreases than increases, but declined for both with increased bin width, albeit at a faster rate for increases (Fig. 6.5). For comparison purposes, we calculated model sensitivity (separately for decreases and increases) for 1000 randomly re-ordered pairs of our observed and predicted $\Delta DE(\%)$, and empirically determined the 95% confidence intervals (i.e. the 25th and 975th ranked classification rates). Sensitivity for the random model ranged around 0.50 (0.38 – 0.55) for the 0 bin width, and also declined with increasing no change bin width, and was consistently higher for decreases than for increases (Fig. 6.5.). Our model's ability to capture actual decreases was significantly greater than the random data across all bin widths. However, in correctly detecting population increases it was less successful and at a 20% no change was not significantly better than the random model.

Conclusion

Our model predictive ability is poor. At a resolution of ± 20%, our best model was only slightly better than picking random numbers and even at the coarsest resolution (only predicting increase or decrease) had a predictive ability of only 75%, a liberal estimate of its accuracy. The addition of a 3rd category, no change, did not improve model accuracy (i.e. predicted changes larger than "sampling error" were no more likely to be accurate). However, model sensitivity, the ability to detect actual changes, decreased with increased no change bin width. The decrease in sensitivity reflects a higher proportion of predicted values being classified as no change with increased bin width, due to the smaller range of predicted population changes compared to observed. This is not a surprising result, since a line of best fit, as was used to generate our model, will always be drawn to the middle of the data range and therefore, will underestimate the extreme data points.

Our model appeared to be even less effective at both predicting and detecting population increases compared to decreases. This lower predictive ability may relate to the absence of factors that directly lead to population increases (recruitment) and a weighting towards down-regulating factors (kill and snow depth).

The 2-category situation (decrease or increase), predicting data for WMU and years used to build the model, represents the best possible situation. If the model were used to predict future data or for another WMU or at a sharper resolution the accuracy of the model would only decrease. Overall our "best model" had very low predictive ability beyond simply predicting increase or decrease.

The inability to accurately predict future population size is not unique to Ontario deer, and has most notably been demonstrated in fisheries-management (Ludwig et al. 1993). This same field introduced many of the basic concepts and techniques commonly employed in deer management (MSY, stock recruitment curves, etc.) and population estimation (CPUE, cohort analysis) (Ricker 1958, Paloheimo 1963, Pope 1972). The large degree of uncertainty in modeling fisheries populations, and past management failures has led to calls for changes in the way populations are managed (Lane and Stephenson, 1999). The effectiveness of traditional reductionist methods of studying the sub-components of population dynamics (age/sex specific demographic rates, predator-prey relationships, intra-specific competition, etc.) in complex systems has been questioned (Cohen and Stewart 1994). Many management agencies have adopted "precautionary" and holistic "ecosystem approaches" into their management plans in acknowledgement of uncertainty in population management to prevent over-harvesting and population collapse (see Department of Fisheries and Oceans, FAO, IECS, etc.).

While deer in Ontario seem unlikely to be over-harvested at current rates, recognizing the uncertainty in deer population predictions may at least allow for more efficient management. From the previous analysis, it is impossible to determine if the poor model fit stems from poor data, the absence of key regulating factors, or inherent stochasticity in deer demographics. Managers are then left to decide if the costs associated with the collection of new or better data are likely to yield a more useful model. An interesting exercise, which may aid in making this determination, would be to review the success of population models in other management areas. If there are few, or no, examples of better predictive population models in other areas of wildlife management (e.g. fisheries, fur harvest, other ungulates, etc.), despite the considerable effort expended in this field, it would seem unlikely that increased effort by the OMNR will yield better results. Regardless, the previous result at least questions the effectiveness of continuing to collect current data in predicting future deer population size and its role in deer management.

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Table 6.1. Comparison of residual mean square (RMS) and standardized partial coefficients for models to predict change in DSPUE (ΔDE), from year t to t+1 versus t + 2 using data in year t or earlier, by WMU groups identified by cluster analysis of WMU mean and maximum values of population density index (d), antlerless kill ($\hat{A}$) and snow depth index (Ws)(as previously described).

Group	ΔDE	*RMS*	Standardized partial coefficients					
			d(t)	*d(t-1)*	*A(t)*	*Ws(t)*	*Ts(t)*	*Tp(t)*
1	t+1	0.006	-0.75	0.59	-0.19	-0.08	0.26	-0.31
	t+2	0.007	-0.79	0.71	-0.38	-0.06	0.12	-0.39
2A	t+1	0.007	-0.60	0.30	-0.01	-0.04	0.32	-0.21
	t+2	0.014	-0.55	0.08	-0.06	0.09	0.29	-0.15
2B	t+1	0.013	-0.68	0.16	0.11	-0.10	0.07	-0.24
	t+2	0.014	-0.63	0.26	0.16	-0.12	0.18	-0.34
2C	t+1	0.010	-0.52	0.25	-0.24	0.06	0.41	-0.33
	t+2	0.012	-0.60	0.21	-0.36	-0.15	0.15	-0.19
3A	t+1	0.011	-0.47	0.08	0.01	-0.12	0.25	-0.10
	t+2	0.014	-0.55	0.03	0.08	-0.09	0.02	-0.12
3B	t+1	0.004	-0.45	0.08	-0.31	-0.20	0.23	-0.16
	t+2	0.006	-0.70	0.22	-0.37	-0.05	0.08	-0.13
4	t+1	0.018	-0.80	0.51	0.07	-0.40	0.17	-0.07
	t+2	0.023	-0.86	0.35	0.14	-0.05	0.05	0.10

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Figure 6.1. Graphic representation of the bin method for assessing predictive ability of our population model. Panel A represents the situation where the observed and predicted values fall into the same bin (i.e. a correct prediction). In panel B, the no change bin width is increased, resulting in the observed and predicted values being assigned to different bins (i.e. an incorrect prediction).

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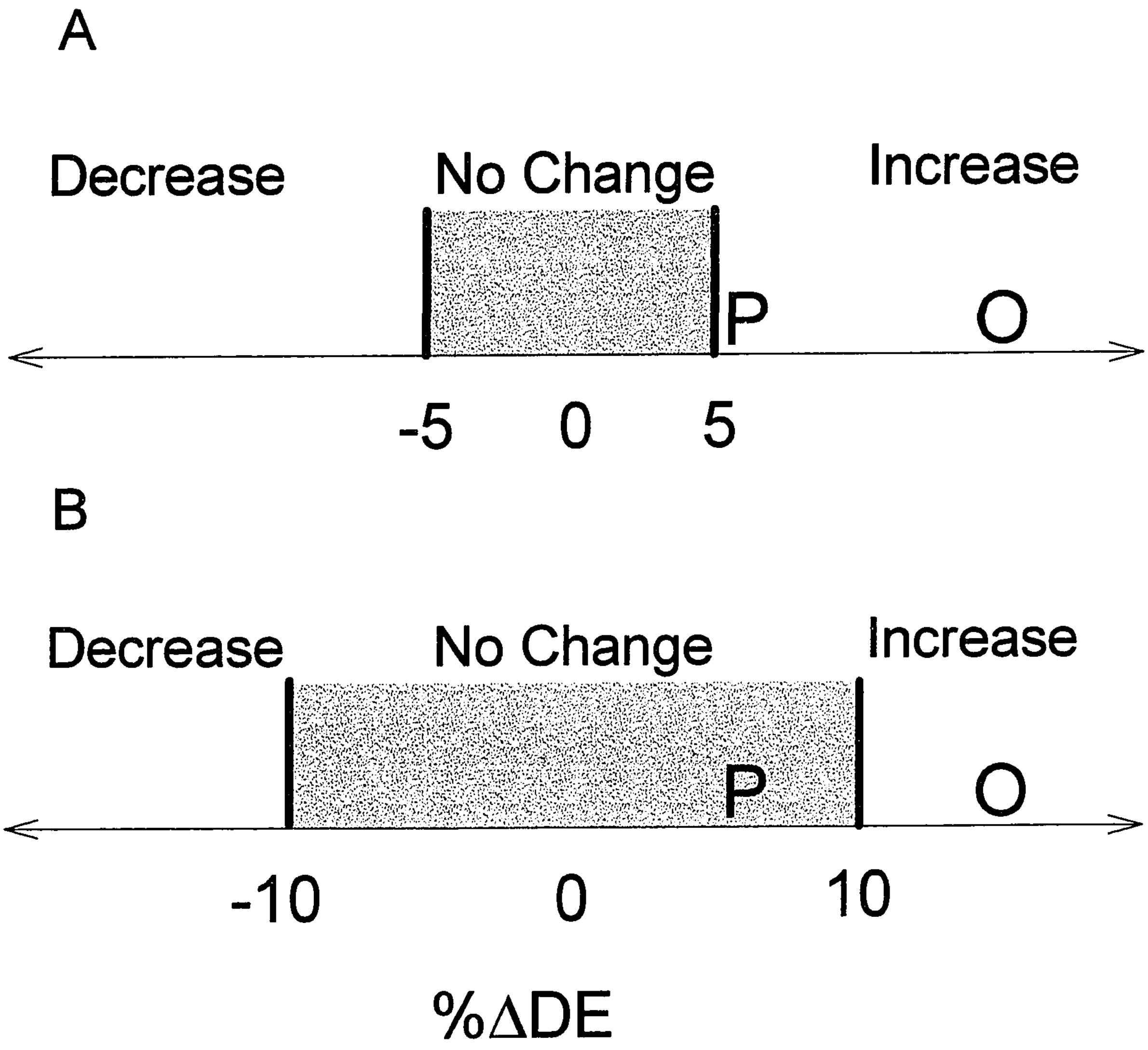

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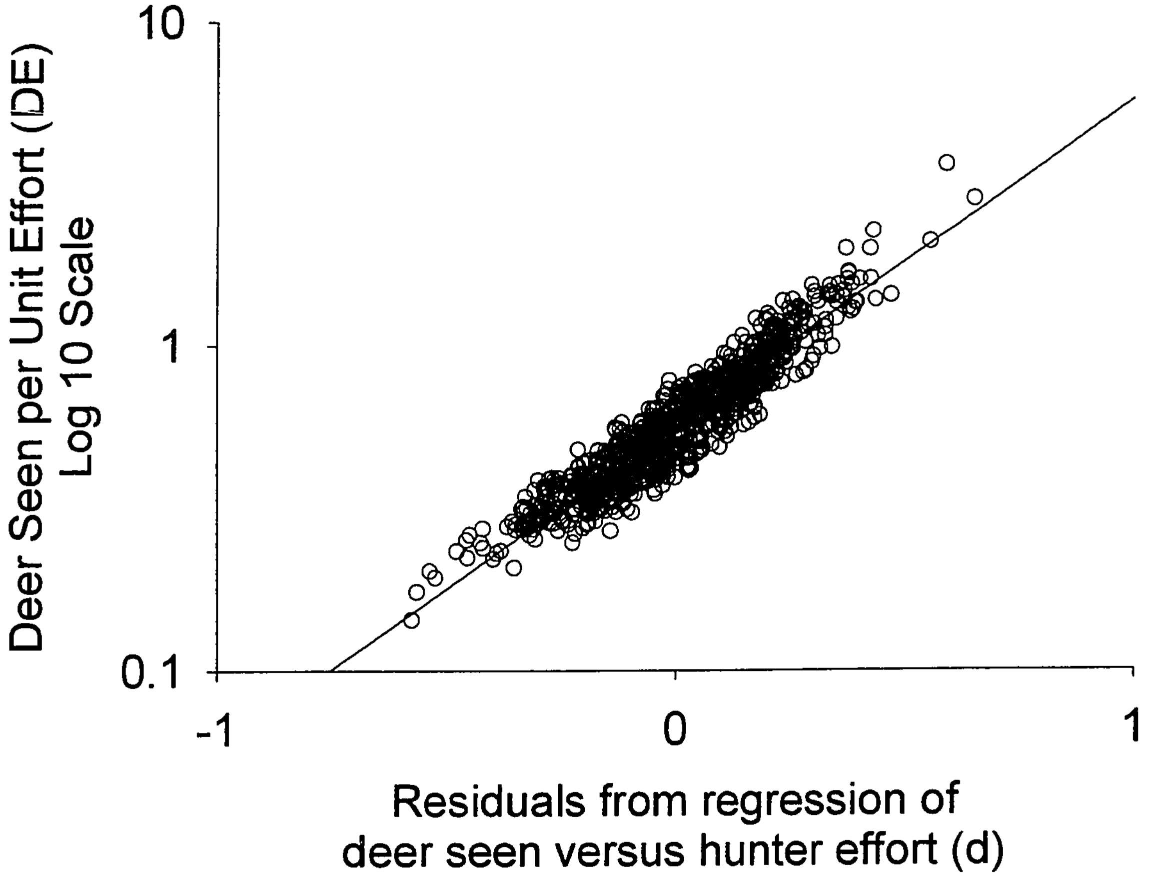

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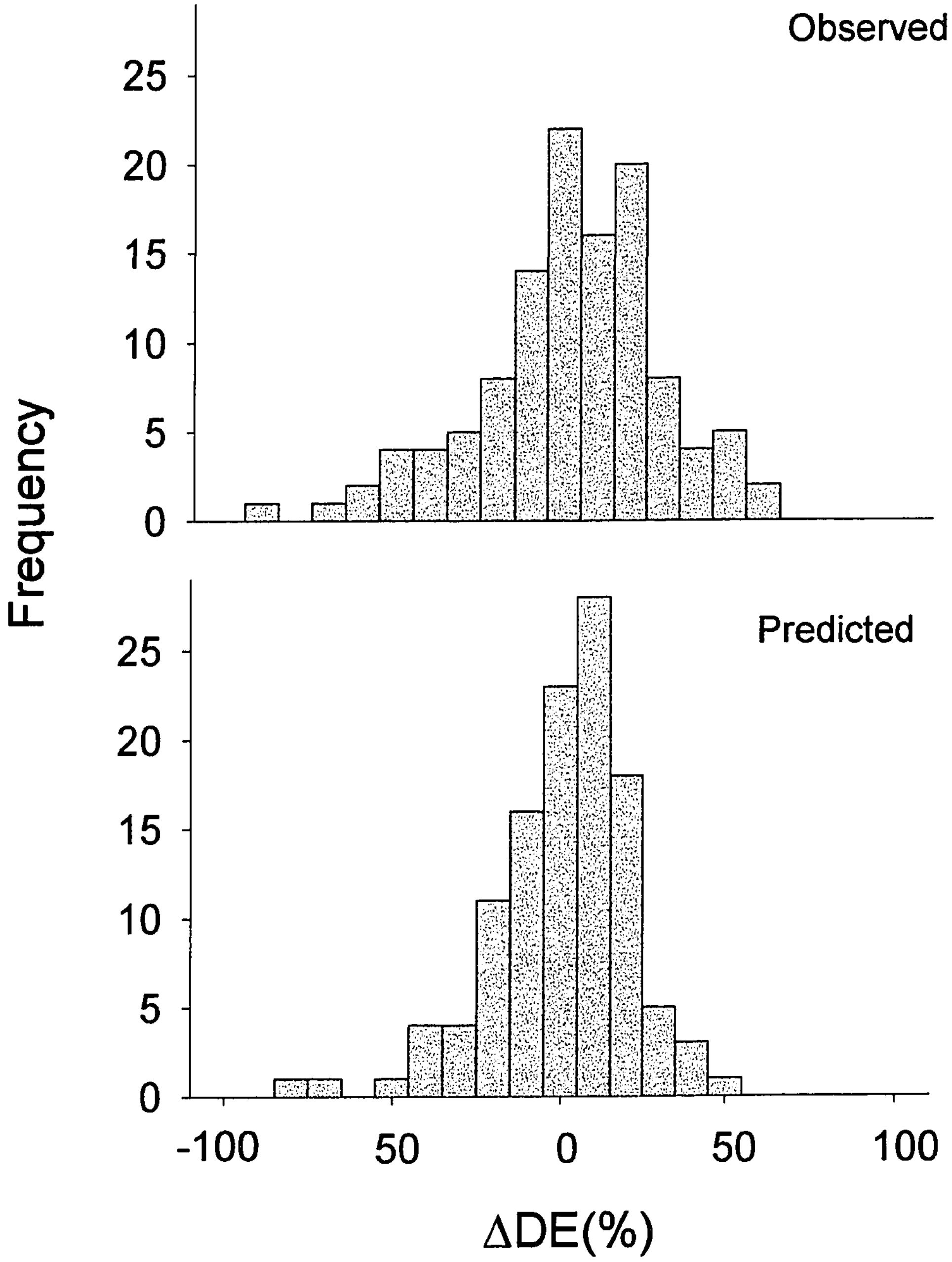

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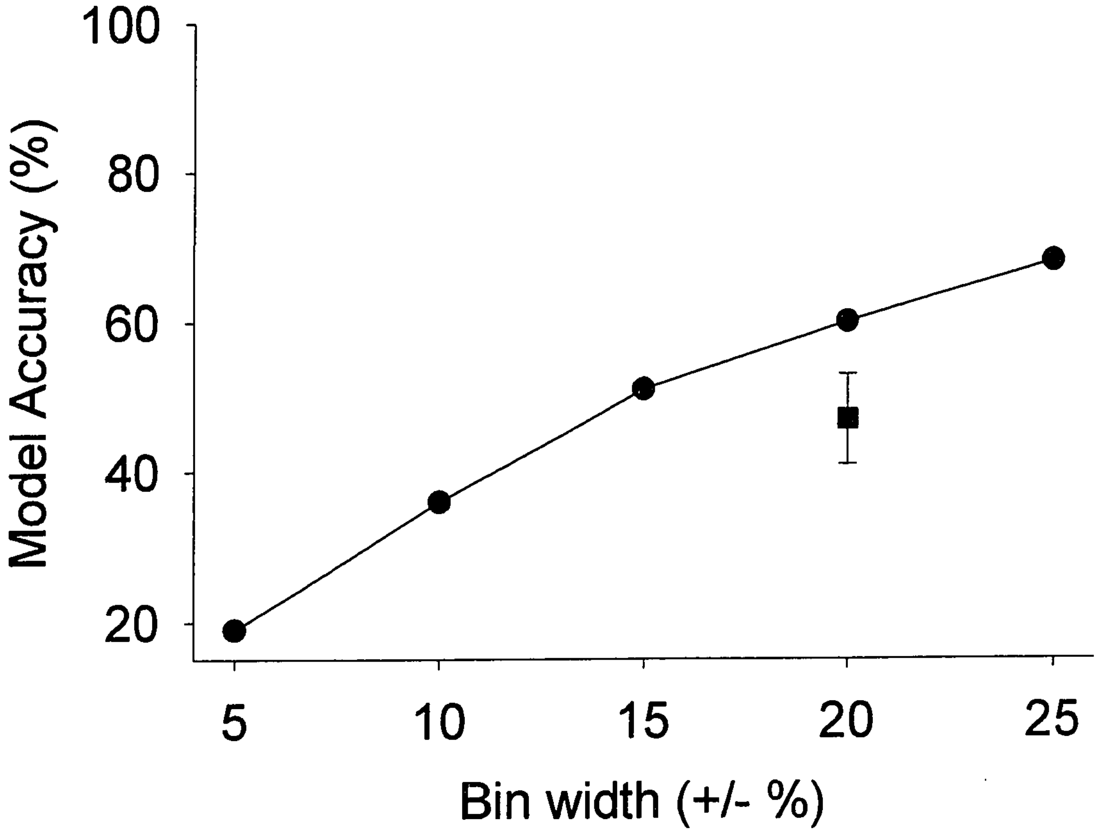

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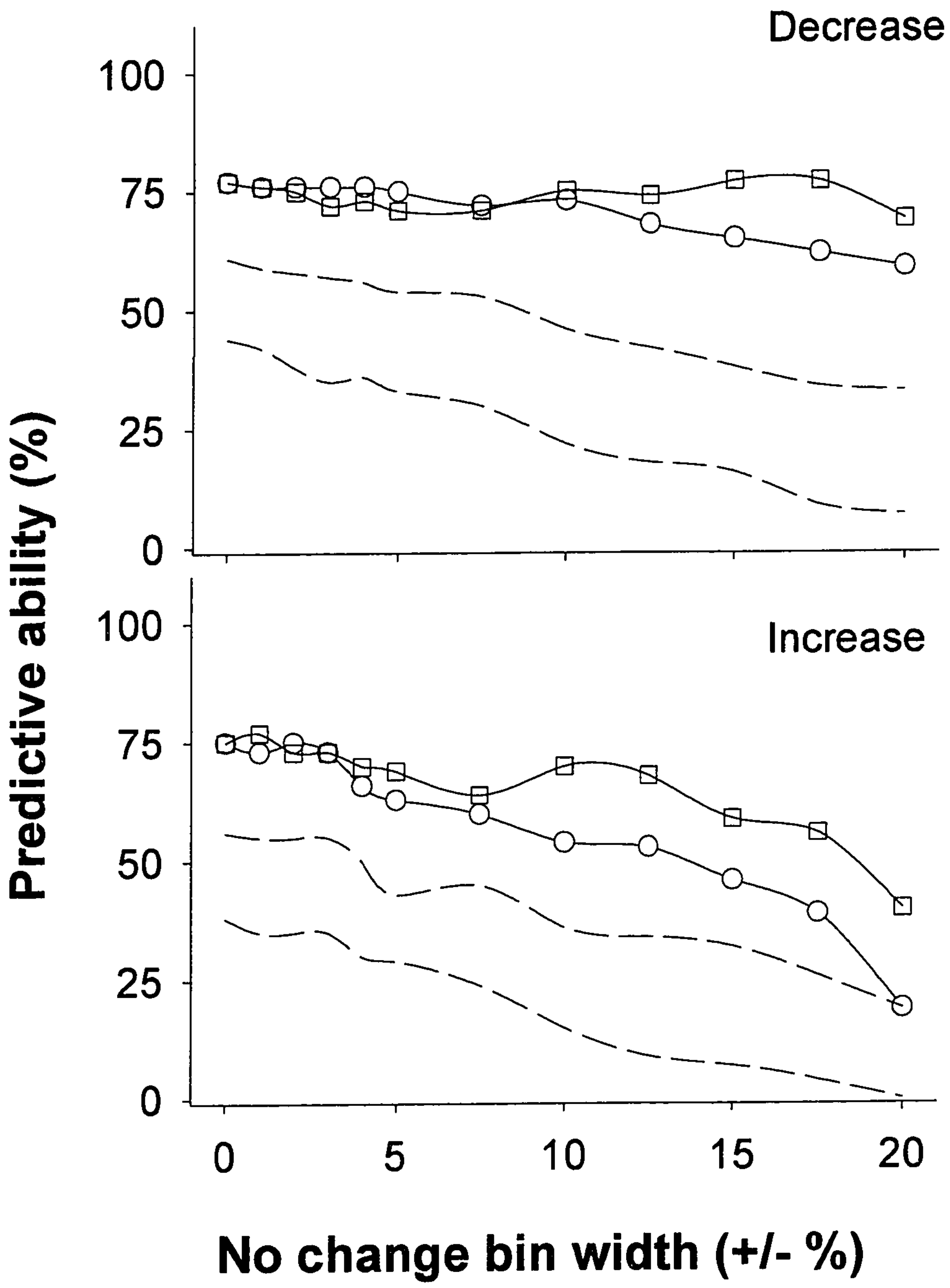

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Chapter 7: Summary of findings and recommendations for white-tailed deer population management in Ontario.

Summary of findings

Our primary purpose for conducting this study was to provide guidance to the Ontario Ministry of Natural Resources towards more effective management of deer populations. Specifically, the goals were to review the historical factors that regulated deer population, evaluate the harvest management systems employed, develop potential methods for easily predicting changes in population and provide recommendations to improve future management and data collection.

To begin, we required an index of deer population that could be used in further analysis. Without a reliable independent measure of population, we were restricted to assessing the potential for putative indices of population to be biased by external factors. Deer seen, controlling for hunter effort, was chosen as our best index of population density, being free of the tag and hunter density biases, which appear to affect indices based on kill. It must be stressed, however, we have no way of determining how well, if at all, deer seen relates to true population size. Therefore, all findings from subsequent analyses contain the caveat that deer seen may bear no relation to actual population density.

We reviewed the effectiveness of historical deer management based on; (1) ability to regulate the size of the deer harvest, and (2) ability of harvest to regulate deer population size, in relation to other factors (e.g. weather, density-dependence). Further, we assessed the consistency of population regulation and management across geographic scales and our ability to predict future population size.

Our analysis of the selective harvest system, the main regulatory system employed in Ontario, concluded that tags only regulated antlerless (and hence total) kill when the proportion of hunters with tags was low (< 40%). Furthermore, regardless of tag level, the number of hunters is an important determinant of kill, and beyond the 40% tag allocation increasing hunter numbers was the only way to increase kill. Additionally, there is evidence hunter success (kill per hunter) may be limited by factors other than population density and tags, possibly related to hunter selectivity and/or demand. Effective management of harvest would appear to best be achieved through controls on hunter numbers and may require management of hunter behaviour.

In regards to the regulation of deer population size we found; (1) historically there was little or no effect of antlerless kill on population, and (2) our ability to predict changes in population, based on currently collected data, is poor. The lack of a kill effect suggests that either historically changes in kill were not large enough to negatively influence population change (i.e. not removing a sufficiently large enough portion of the population to down regulate), or that any kill effect or "signal" was being obscured by the "noise" introduced by data error in model.

The poor predictive ability of our model may be due to a combination of (1) the omission of key factors in controlling population regulation, (2) poor data quality, (3) a poor or no relationship between our index of population and true population size, or (4) deer populations are inherently stochastic and cannot be accurately modeled. With no way of determining which of these factors are responsible for our poor predictive ability, there is no guarantee the collection of new or better data will not improve the model fit. We may be accurately measuring all the factors that regulate population but if our population index does not relate to true population size then our model will not be accurate. Further a review of attempts to predict population in other fields (e.g. fisheries management) may suggest that improved data collection or models are unlikely to yield better predictive ability. Regardless of the cause of the poor predictive ability, one might question the effectiveness of continuing to collect the same data in the same fashion.

In light of the findings above, attempts to micro-manage deer populations within some tight population range, through small changes in tags and/or hunters, will not be successful. Managers will be unable to predict the result of small-scale changes in kill on population, which instead will fluctuate unpredictably in relation to population size, weather factors and possibly other unknown factors. It would appear that the current system of fine-scale management of tags to control harvest, will continue to be unsuccessful in predictably, managing deer populations.

Recommendations for future management

Population management

Deer managers are not alone in having to incorporate uncertainty, both of population size and the factors that regulate it, into management plans. Other fields are currently struggling with historical failures in population management, due in part to poor predictive ability (Ludwig et al., 1993). A notable local example is the collapse of the Atlantic cod fishery, which led to a fishing moratorium in 1992 that remains in place today. Despite the large amount of effort applied to its study, the cause of the collapse remains unknown, though over-harvest is often cited (Hutchings and Myers, 1994). In order to avoid a repeat of the past failure, new management plans are being proposed that incorporate uncertainty and the inability to accurately predict population changes (Lane and Stephenson, 1999). Rather than constructing complex models to predict specific levels of harvest (i.e. maximum sustained yield), managers are being advised to look to minimize risk and manage to avoid catastrophe. Further, the efficiency of continuing to research deeper into the sub-components of a system, with a view to building better models, is questionable in light of the historical failure of this approach to produce better predictive ability, especially as you move farther from the scale at which the system is managed (Lane and Stephenson, 1999).

The Fisheries Resource Conservation Council (FRCC) has recently proposed a coarse scale or "***quantum management***" plan for 4X5Y atlantic cod stocks (FRCC, unpubl.)(Table 7.1). Under the proposed system, broad population ranges, based on Spawning Stock biomass, are established, and a fixed harvest quota (in tonnes) is set for each range. As long as the estimated population remains with a range, the yearly quota is unchanged. If population size moves into a new range, then quotas are changed to the corresponding, pre-determined value. Population ranges are quite broad, reflecting the inability to accurately predict population size (i.e. the true value may vary considerably from the estimated). Further, the differences between quotas are large resulting in few, but significant, changes in harvest, thereby eliminating attempts to fine-tune harvest and population. The quotas, established in consultation with fisherman, are relatively conservative (the top being 10,000 which is well below the historical peak annual harvests of > 100,000 tonnes), even when fish appear plentiful, in order to protect against repeat of the population collapse. Additionally, this system is operationally simple to apply and provides a consistency in harvest quotas, which facilitates budgeting and planning by the fishing industry.

For deer, over-harvesting leading to population crashes is less of a concern, but there are still benefits to be derived from this type of system. The goal in deer management would be to maintain deer population (or an index of population) within an acceptable range, the limits of which would be determined for each WMU according to its needs (Fig. 7.1). When estimated population size exceeds the limits, the appropriate management action is taken (i.e. changes in tags, hunter numbers, season length, etc.) to drive the population back into the desired range, and a return to the previous management situation.

Quantum management of deer would eliminate most of the effort spent each year setting and implementing small changes in tag quotas, which historically had no detectable effect on population. As long as population (or an index of population) remains within the pre-determined limits tags remain unchanged, as it is unlikely the outcome of such a change could be predicted. When population size moves out of the acceptable range, indicating a serious threat (i.e. too low or overabundance), large management changes (i.e. large changes in kill) are enacted, which have a greater likelihood to produce predictable effects on population and allow for adaptive management and refinement of harvest limits. Hunters and outfitters may also benefit from more consistent and predictable harvest quotas for planning future hunts and business.

Setting population limits

The key to such a system will be determining the acceptable range of population. Deer population size itself is rarely the true endpoint of interest in deer management. Rather, deer are managed for some factor related to population, such as hunter satisfaction, nuisance problems, plant communities, etc. Once the true management endpoint is established, managers can then determine its relationship with population or more importantly some index of population (e.g. DSPUE). By looking at historical ranges of DSPUE, we may be able to determine levels at which there were observable changes in the true endpoint. For example, at what level of DSPUE did hunters complain about low population levels or lack of success? If our endpoint (e.g. hunter satisfaction) remains essentially the same at the upper and lower historical limits, active management may be unnecessary. Managers need only monitor populations to ensure they are remaining within their historical limits, and only when the population fails to react as predicted at the extremes (i.e. does not return to center) will management action be required.

Setting harvest quotas

Determining the appropriate harvest quotas, for the different population zones would be an adaptive process, with the results of previous kills used to refine future quotas. Tags can be used to restrict kill to low levels, and historically low kills appear to have contributed to large population growth in the early 1980's. Antlerless kill, however, only showed an ability to down regulate kill in WMU with relatively high kill but low population density. In the other WMU, harvest was apparently not removing a large enough proportion of the population to suppress growth. Managers in these WMU will have to consider the lack of regulatory effect for historical kills when setting new quotas. Some guidance may be extracted by empirically comparing the size of the kill, in relationship to population, for those WMU that showed a significant negative effect of kill.

Other factors to consider are the apparent limitation of tags once 40% of hunters have tags, and the strong effect of hunter numbers on kill. Where current levels of hunter participation are not sufficient to down-regulate deer populations, managers may have to find methods of encouraging hunter participation or improving hunter efficiency. Hunter selectivity or demand may be limiting kill and managers may need to provide incentives to take more deer. Recently, some southern WMU with high deer densities have begun allowing hunters to apply for a second deer license in an attempt to increase kill (Margaret McLaren OMNR, pers. comm.). This option would seem promising as it (a) allows the more efficient, avid hunters to take more deer and (b) potentially reduces selectivity due to hunters passing on earlier deer in order to prolong their hunting opportunity or to save their only deer for the "trophy" deer that may never come.

Data collection

The main problems with the survey data are (1) low sample sizes of returned surveys, especially in lightly hunted areas and (2) the time required to process the results. Our ability to predict population changes, while already poor, will only be further lowered by inaccurate data or the necessity of predicting more than 2 years ahead due to delays in receiving the latest results. The results of the now discontinued PMS often took years to be analyzed and returned to managers, at which point the already questionable information was of even less value.

The Post Card Survey, currently the only source of data for selective harvest, provides faster information, but is limited insofar as it only surveys tag holders and does not provide estimates of deer seen. Any new survey, for deer management purposes, should be designed to provide results prior to setting the following year's harvest quotas and should include both deer seen and killed, along with a measure of hunter effort and numbers. The current, non-systematic collection of deer physical (e.g. YABD) and productivity data (e.g. embryos per doe), does not appear to provide any guidance to managers in terms of assessing current or future population size, and one must question the usefulness of continuing to collect data in this manner.

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Lane, D.E. and Stephenson, R.L. 1999. Fisheries-management science: a framework for the implementation of fisheries-management systems. IECS Journal of Marine Science. 56: 1059-1066.

Ludwig, D., Hilborn, R. and Walters, C.J. 1993. Uncertainty, resource exploitation, and conservartion: lessons learned from history. Science. 260: 36-37.Ludwig et al.

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Table 7.1. Quantum management system proposed by the Fisheries Resource Conservation Council (FRCC) for 4X5Y atlantic cod stocks. For each population range, measured by Spawning Stock Biomass (SSB) (tonnes) there is a pre-determined harvest quota (tonnes).

Population (SSB in tonnes)	Harvest Quota (tones)
< 30,000	fishery closed
30-40,000	6,000
40-50,000	8,000
50-60,000	10,000

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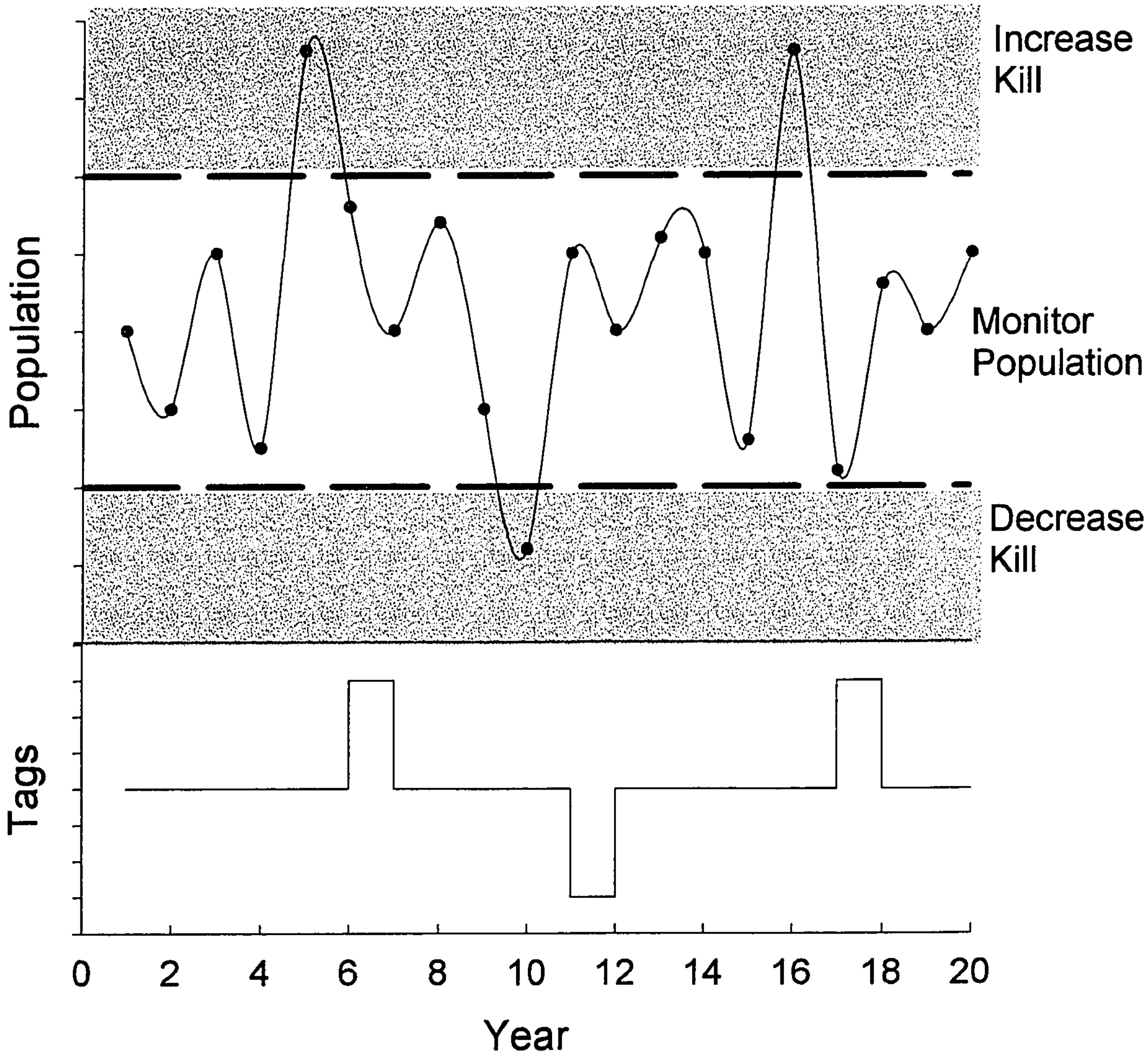
Figure 7.1. Hypothetical deer population time series demonstrating proposed Quantum Management Plan. When population is desired population range (white zone), tags (or some other management tool) are not changed. Only when population leaves the desired range and enters a new range (yellow zones) are management actions applied (e.g. increase or decrease kill through issuing of tags). The lower panel demonstrates changes in tag quotas (or some other management tool).



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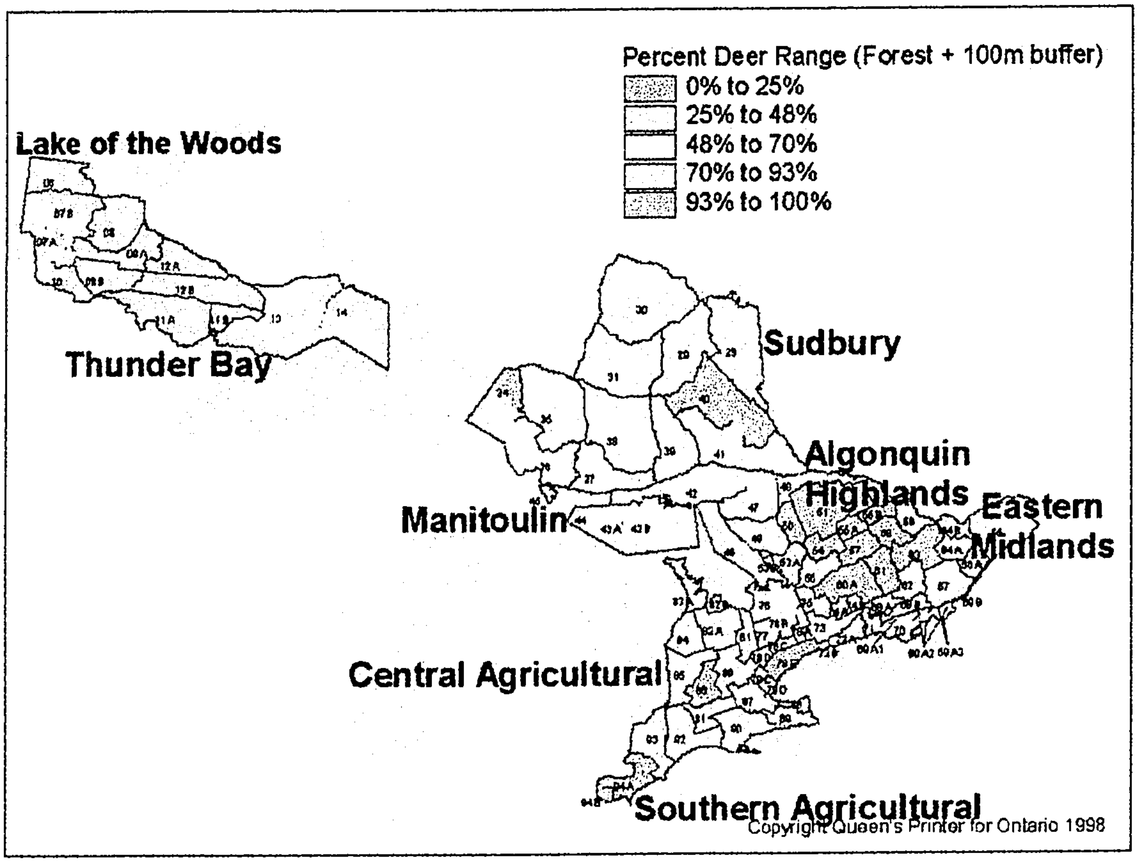
Appendix 1. Map showing Wildlife Management Units (WMU) and Deer Management Areas (DMA) in Ontario, along with the estimated percent deer range. Taken from Ontario Deer Model CD-ROM produced by the Ontario Ministry of Natural Resources.



Appendix 2: List of all variables used in the study, the factor they describe, their description and their source.

Variable	Factor	Description	Source
*Harvest**			
R	Number of Survey Respondents	Total number of surveys returned by hunters	PMS
$\widehat{D}$	Doe Kill	Total does killed extrapolated from hunter reports	PMS
$\widehat{B}$	Buck Kill	Total bucks killed extrapolated from hunter reports	PMS
$\widehat{F}$	Fawn Kill	Total fawns killed extrapolated from hunter reports	PMS
$\widehat{A}$	Antlerless kill	Total antlerless deer (fawn +doe) killed extrapolated from hunter reports	PMS
$\widehat{K}$	Total Kill	Total deer killed extrapolated from hunter reports	
$\widehat{H}$	Hunters	Extrapolated total number of hunters	PMS
$\widehat{E}$	Effort	Extrapolated total number of days hunted	PMS
$\widehat{S}$	Deer seen	Total deer seen extrapolated from hunter reports	PMS
Physical			
ED	Embryos per doe	Number of embryos per hunter killed doe recorded at check stations	BGM
LD	Proportion of lactating does	Proportion of hunt killed does that showed signs of lactation	BGM
FD-H	Fawn: Doe from Hunters	Ratio of fawns to does killed, reported by hunter surveys	PMS
FD-C	Fawn: Doe at Check Station	Ratio of fawns to does killed, for deer sexed at check stations	BGM
Y	Yearling antler beam diameter	The diameter (mm) of antlers for 1-year old (yearling) male deers	BGM
Weather			
R_P	Spring Rain	Total rainfall (mm) from April - May	EC
R_S	Summer Rain	Total rainfall (mm) from June - August	EC
T_P	Spring temperature	Average temperature (°C) from April-May	EC
T_S	Summer temperature	Average temperature (°C) from June-August	EC
Tw	Winter temperature	Average temperature (°C) from November – March	EC

W_S	Snow depth index	Cumulative total of the weekly average snow depth (cm)	SNOW
Hunt Conditions			
DS	Days with Snow	Number of days during the hunt with snowfall	EC
DR	Days with Rain	Number of days during the hunt with rainfall	EC
DB	Days below 0 °C	Number of days during the hunt where temperature was below 0 °C	EC
CS	Snow during hunt	Average snowdepth (cm) during the hunt	EC
CR	Rainfall during hunt	Average rainfall (cm) during the hunt	EC
CT	Temperature during hunt	Average temperature (°C) during the hunt	EC
L_F	Total Forest	Total forested area in a WMU (km^2)	OLC
Derived			
d	Population index	Residual from regression of log 10 deer seen ($\hat{S}$) versus log 10 effort ($\hat{E}$)	---
DE	Population index	Deer seen per unit effort (DSPUE)	---
θ	Hunter Density	Number of Hunters ($\hat{H}$) / km^2 of forest (L_F)	---
ρ	Proportion of hunters with tags	Tags (P) / Hunters ($\hat{H}$)	---
α	Antlerless kill per hunter	Total Antlerless Kill ($\hat{A}$) / Hunters ($\hat{H}$)	---
β	Buck kill per hunter	Total Buck Kill ($\hat{B}$) / Hunters ($\hat{H}$)	---
σ	Deer seen per hunter	Total Deer Seen ($\hat{S}$) / Hunters ($\hat{H}$)	---
λ	Antlerless proportion of harvest	Total Antlerless kill ($\hat{A}$) / Total Kill (K)	---
ΔA	Change in antlerless kill	$\hat{A}$ (t+1) – $\hat{A}$ (t)	
ΔH	Change in number of hunters	$\hat{H}$ (t+1) – $\hat{H}$ (t)	
ΔP	Change in number of tags issued	P(t+1) – P(t)	
Δd	Change in population index	d(t+1) – d(t)	
ΔDE	Change in population index	DE(t+1) – DE(t)	

* Caret denotes variables extrapolated to all hunters from surveys returned (e.g. $\hat{K}$)