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MOVEMENTS, SURVIVAL, AND MORTALITY OF WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY

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TABLE OF CONTENTS

TABLE OF CONTENTS II

LIST OF TABLES III

LIST OF FIGURES IV

EXECUTIVE SUMMARY V

INTRODUCTION 1

STUDY AREA 5

METHODS 8

- Capture and Radiotelemetry 8
- Summer and Winter Range Identification 8
- Seasonal Migration Direction and Distance 9
- Mortality 10
- Survival Analysis 10
- Population Modeling 11

RESULTS 12

- Captures 12
- Migration 12
- Mortality 13
- Seasonal Mortality 14
- Population Growth and Estimated Density 15

DISCUSSION AND MANAGEMENT IMPLICATIONS 15

RECOMMENDATIONS 20

LITERATURE CITED 23

LIST OF TABLES

Table 1. Number of deer radiocollared, radiodays accumulated, and annual survival for each year of study in south-central British Columbia, 1988-2001. 28

Table 2. Results of Manly's test of resource selection. A score significantly above or below 0.125 suggests preference or avoidance respectively. 29

Table 3. Number of mortalities (associated cause specific annual mortality rate), and annual survival rates of female white-tailed deer in the Pend D'oreille river valley British Columbia, 1988-2000. 30

Table 4. Seasonal mortality totals and rates for female white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988–2001. 31

LIST OF FIGURES

FIGURE 1. DENSITY DEPENDENT BIRTH, MORTALITY, GROWTH RATES, AND RESULTING POPULATION. NOTE THAT AS THE MORTALITY RATE SURPASSES THE BIRTH RATE THE GROWTH RATE DECREASES BELOW 1.0 (K) AND THE POPULATION DECLINES. 32

FIGURE 2. PEND D'OREILLE VALLEY WHITE-TAILED DEER WINTER RANGE STUDY AREA 33

FIGURE 3. MIGRATION DIRECTION AND DISTANCES OF FEMALE WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY BRITISH COLUMBIA 1987-2000. 34

FIGURE 4. ANNUAL SURVIVAL RATES AND ASSOCIATED 95% CONFIDENCE INTERVALS FOR WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY 1988 - 2000. 35

FIGURE 5. CAUSE SPECIFIC MORTALITY RATES FOR FEMALE WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA 1988–2000 (NOTE THAT THE X-AXIS FOR UNKNOWN MORTALITIES HAD TO BE INCREASED TO FIT THE 1998 RATE). 36

FIGURE 6. SEASONAL CAUSE SPECIFIC MORTALITY AND SURVIVAL RATES FOR FEMALE WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA 1988–2001. 37

FIGURE 7. ESTIMATED POPULATION GROWTH RATES FOR WHITE-TAILED DEER IN THE PEND D'OREILLE VALLEY 1988 – 2000 BASED ON HIGH (0.68), MEDIUM (0.31), AND LOW (0.18) FAWN SURVIVAL (THE SOLID LINE MARKS A STABLE POPULATION LEVEL $\lambda = 0$) .. 38

FIGURE 8. ESTIMATED WHITE-TAILED POPULATION DENSITIES FROM 1988 TO 2001 IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA. 39

FIGURE 9. COMPARISON OF THREE POPULATION INDICIES FOR WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA 1988 - 2001. 40

FIGURE 10. POPULATION GROWTH RATE PLOTTED AGAINST ESTIMATED DENSITY OF WHITE-TAILED DEER FOR THE PREVIOUS YEAR IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA 1988 – 2001. THE NEGATIVE SLOPE DENOTES A SLOWING GROWTH RATE AS THE POPULATION INCREASES AND THUS DENSITY DEPENDENCE. 41

FIGURE 11. CAUSE SPECIFIC MORTALITY RATES PLOTTED AGAINST ESTIMATED POPULATION FOR WHITE-TAILED DEER IN THE PEND D'OREILLE RIVER VALLEY OF BRITISH COLUMBIA 1988 – 2000 42

FIGURE 12. COMPARISON OF WHITE-TAILED POPULATION, THE NUMBER OF DOE TAGS ISSUED, AND THE NUMBER OF DOES HARVESTED. 43

EXECUTIVE SUMMARY

White-tailed deer overabundance is becoming a major issue for wildlife managers across North America. In British Columbia, it has been recently suggested that abundant white-tailed deer may contribute to increasing populations of generalist predators that in turn may negatively impact secondary or alternate prey populations. We examined 14 years of white-tailed deer telemetry data collected by the Columbia Basin Fish and Wildlife Compensation Program. The purpose of this study was to establish mortality, population and migrational trends of deer using the Pend d'Oreille River winter range in south-central British Columbia. From 1988 to 2001 we radiocollared 63 white-tailed deer and documented 40 mortalities. Over the course of the study, the mean annual survival rate was 0.7680. The main cause of known mortality was cougar predation (0.069), followed by vehicle accidents (0.046), hunting (0.028), poaching (0.023) and natural causes (0.023). Cougar predation and natural mortality appear to be density dependent (increasing with increased population) while hunting, poaching, and vehicle accidents appear to be inversely density dependent (increasing as the population decreases). Seasonal mortality rates were essentially equal although slightly higher during winter. By our model, the population reached a high in 1992, declined until 1995, and rebounded from 1996 to 2001. The white-tailed deer that winter in the Pend d'Oreille valley migrate 360º to summer ranges. All but one collared deer was migrational. North-northeast, and east-northeast directions were preferred, while south-southeast and west-northwest were avoided. As a result, habitat enhancement targeted at other ungulate species may also benefit this migratory whitetail population. Our data suggests that doe harvest may be an effective tool in helping to reduce white-tailed deer densities. Limiting whitetail populations through increased doe harvest may be the best management strategy left to managers, and should be investigated through modeling or empirical study.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) have become a challenging management issue across North America. In fact, the success of wildlife managers in growing populations of white-tailed deer, has now led to one of the most challenging problems in wildlife management; whitetail overabundance (Warren 1997). It is generally believed that white-tailed deer populations are currently at densities exceeding historical levels (Knox 1997) and are increasing (Crete and Daigle 1999).

Whether or not white-tailed deer are overabundant can be a subjective observation left to individual managers who base their opinion on personal observation or public perception. A more objective definition of local overabundance may be when whitetail numbers begin to interfere with normal ecosystem function by suppressing other plant and wildlife populations (Caughley 1981). In eastern North America white-tailed deer have a substantial impact on plant morphology, seedling establishment and the structure of plant communities (Waller and Alverson 1997, Russell et al. 2001). In British Columbia, it has recently been suggested that abundant white-tailed deer and other ungulate prey are increasing populations of generalist predators, that in turn may negatively impact secondary or alternate prey populations (Seip 1992, Kinley and Apps 2001, Robinson et al. 2002).

Population regulation and limitation have been the subject of a great deal of research in ecology and are closely related to the concept of ecological carrying capacity (*K*)

(McCullough 1992). Simple models demonstrate how a population will trend towards carrying capacity until survival and birth rates slow because of limited resources, resulting in a slowing growth rate (Figure 1). Whitetails, in the absence of predators, are approaching K in the Northeastern United States (Conover 2001).

In several ungulate studies, predation has been found to be a major source of adult mortality (Bleich and Taylor 1998) and may be capable of regulating a prey population (Messier 1994). A regulating factor is one that returns a population to an equilibrium point through density-dependent forces (Caugley and Sinclair 1994:115, Sinclair and Pech 1996). By definition this can only hold true in single predator/single prey systems where there is a direct tie between predator and prey (i.e. predators increase as prey density increases, and decrease as prey density decreases). It is more likely that predation, especially in multi-predator/multi-prey systems, simply limits populations by increasing adult mortality. A limiting factor is one that simply causes a change in population production or loss (Caugley and Sinclair 1994:115). Kunkel (1997) found predation to be a major limiting factor of white-tailed deer and elk in a multi prey/multi predator system.

Most management activities are directed at population limitation, or those factors directly related to limitation. Managers have often used feeding programs, and sport harvest of both deer and predators to control deer mortality and therefore populations. When deer numbers decrease, predators are removed to help increase survival (Carpenter, 1998).

Although only limited research has been conducted on the effect of doe harvest on deer populations, managers to reduce (limit) deer density often use this strategy.

Habitat management (fire suppression, timber harvest, etc.) may affect carrying capacity and therefore may be more likely to approach regulation. Controlled attempts at using large scale habitat management to regulate deer populations is complicated by individual deer behaviours such as seasonal habitat use and migration. Migration is thought to provide individuals within a population, with increased foraging opportunities, escape from extreme seasonal environmental conditions, and decreased predation pressure (Brower and Malcolm 1991, Krebs 1994:471, Morrison et al 1998:21). As such, patterns of migration have vast ramifications on reproduction, survival, and population growth, and therefore the management of wildlife species (Morrison et al 1998:19). Further, seasonal migrations of white-tailed deer into the traditional ranges of other ungulate species may draw generalist predators into those areas. This increased predator density may in turn increase mortality of secondary prey (Katnik 2002, Siep 1992).

Deer populations often show a combination of migratory and resident individuals. Mackie et al (1998:40) described three distinct movement patterns of mule and white-tailed deer: residents, where seasonal home ranges have a high degree of overlap; adjacent seasonal home ranges that are separated by a few kilometres; and distinct seasonal home ranges where the distance between seasonal home ranges can be as much as 130 kms.

Exclusively resident populations may indicate habitats where all an animal's seasonal needs (maintenance and reproduction) can be met, or where no measurable gain can be attained through migration (Mackie et al 1998:43). Migration can provide for increased foraging opportunities, however this advantage may come at the cost of increased predation pressure. Nicholson et al. (1997) found that migratory mule deer were subjected to increased predation during migration. The relationship between migration and mortality is further complicated by timber harvesting practices. For instance on Vancouver Island where logging had removed most old growth stands at low elevations, McNay and Voller (1995) found that non-migratory deer were more prone to predation and recommended that maintaining old intact forests at low elevations was basic to rebuilding deer populations on Vancouver Island.

We conducted a retrospective study of 13 years of white-tailed deer telemetry data. The purpose of this study was to establish population and migrational trends of deer using the Pend d'Oreille River winter range in south-central British Columbia. An increasing white-tailed deer population may impact other ungulate populations in the area through both direct competition for resources, and indirect competition by increasing the numbers of predators in the area. Our first goal was to determine white-tailed deer mortality (limiting factors) and population trends. We developed population trend data by calculating annual adult female survival rates and using these rates, a fixed maternity rate, and a high, medium and low fawn survival rate in a Leslie Matrix (Leslie 1945). Annual growth rates were then used to project three population densities for each year based on a known density obtained through aerial survey in 1999. Cause specific mortality rates were then plotted against these projected densities to gain insight into whether or not any showed density dependence. As seasonally migratory deer may also lead generalist predators into overlapping areas with other ungulate species, our second goal was to determine migration patterns of deer wintering in the Pend d'Oreille River valley.

Study Area

The study area covers approximately 4,950 ha on the north bank of the Pend d'Oreille River southeast of Trail, adjacent to the Canada/USA border (Figure 2). It encompasses all the white-tailed deer winter range as designated in the late 1970's using local knowledge and radiocollared animals (Woods 1984). White-tailed deer are the primary ungulate species wintering in the valley. Elk (*Cervus elaphus*) are present in much lower numbers (Woods 1983). Mule deer (*Odocoileus hemionus*) winter on a relatively small portion of the winter range above the confluence of the Salmo and Pend d'Oreille Rivers and in the upper reaches of Grouse Creek (J. Gwilliam, unpublished data). White-tailed deer wintering in the study area utilize summer range covering over 2,500 km^2, primarily east, north and west, but also south of the study area (Woods and Woods 1979, Woods 1983, 1984).

The study area encompasses southern aspects and relatively steep slopes on the north side of the Pend d'Oreille River. Elevations range from 470m along the Pend d'Oreille River area is within the Interior Cedar Hemlock (ICH) biogeoclimatic zone, including the xeric, warm (xw) subzone in the valley bottom, dry, warm (dw) on lower to mid-elevation slopes, and moist, warm (mw) at midslope (Meidinger and Pojar 1991).

Douglas-fir (*Psuedotsuga menziesii*) commonly dominate southern exposures, much of it even-aged stands that resulted from a major fire in the 1890's (Vold et al. 1980, Woods 1984). Shrub or grass communities with open Douglas-fir or ponderosa pine (*Pinus ponderosa*) stands occupy steep south aspects influenced by fire. Western redcedar (*Thuja plicata*) and grand fir (*Abies grandis*) prevail throughout lower and mid-elevation moist sites. Lodgepole pine (*Pinus contorta*), western white pine (*Pinus monticola*) and western larch *(Larix occidentalis*) are found on some sites. Deciduous species include white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*).

Cougars (*Puma concolor*) are the primary predators of ungulates wintering in the study area, however, coyotes (*Canis latrans*) are also common. Kootenay Wildlife Management Unit 4-08 covers approximately 90% of the summer range used by the white-tailed deer that winter in the Pend d'Oreille valley (BC Environment, Lands and Parks harvest statistics). Within management unit 4-08, human harvest of white-tailed deer averaged 265 animals (σ = 135, range 46 - 518) annually between 1983 and 1999. The British Columbia Ministry of Water, Land and Air Protection (MWLAP) allowed a limited doe season within the study are until the end of 1997. Doe harvest was not allowed in 1998 or 1999, but was reintroduced in 2000.

The climate of the area is transitional between wetter temperate coastal and drier continental weather patterns. Mean July and January temperatures for Waneta, located in the valley bottom at the west end of the study area, are 19.7 and –4.8 °C, respectively (Vold et al. 1980). Annual precipitation at Waneta averages 630 mm, with 180 cm falling as snow. Total precipitation within the valley increases from west to east and with increasing elevation (Vold et al. 1980). Snow often persists on the valley floor from early December to mid-March, but during mild winters low elevation south-facing slopes may be snow-free for periods during mid-winter.

In addition to natural succession, the Pend d'Oreille valley has been influenced by a number of disturbances. Construction of the Waneta Dam near the mouth of the Pend d'Oreille River in the mid-1950's flooded approximately 7 km of river and 175 ha of valley bottom (Vold et al. 1980). The Seven Mile Dam 15 km upstream flooded a further 14 km of river and 212 ha after construction in 1979 and again in 1988 when the reservoir level was raised 5 m. There is approximately 54 km of transmission lines within the study area, directly affecting about 250 ha of habitat. Harvesting (primarily Douglas-fir) of forests has occurred over portions of the area. Wildfire, historically the most important natural disturbance, has been suppressed over much of the past century, such that few natural fires have occurred since the 1930's (Woods 1984). Habitat management has occurred in the valley, including several prescribed burns up to 70 ha in size, shrub-cutting to rejuvenate decadent shrubs and to promote the growth of young Douglas-fir and ponderosa pine, some planting of Douglas-fir seedlings, and control of noxious weeds (J. Gwilliam unpublished data).

METHODS

Capture and Radiotelemetry

White-tailed deer were captured on the primary winter range of the West Kootenay in the Pend d'Oreille River valley. Most deer were captured in collapsible Clover-type deer traps (Clover 1956) during 1989-99. Each winter 5 or 10 traps were operated from mid-January to March. Several deer were also captured in February 1999 and March 2001 using an aerial net-gun from a Hughes 500 helicopter (Barret et al. 1982).

Adult does, female fawns and one young buck were fitted with radiotelemetry collars (LMRT 3: Lotek Inc., Newmarket, Ontario, Canada). Two male fawns were fitted with expandable collars (MOD 500: Telonics, Mesa, Arizona). Radiotransmitters had an estimated 4-5 year battery life and were equipped with motion-sensitive mortality sensors with a 6-hr delay.

Radiocollared deer were relocated 1-2 times weekly using a combination of ground and aerial telemetry. Aerial relocations were obtained from a Cessna 337 fitted with 2 strut-mounted directional antennas.

Summer and Winter Range Identification

Coordinates (Zone 11, NAD 83) for the winter range locations were determined by mapping the capture sites on the appropriate 1/20,000 forest cover map. Coordinates for summer range locations were determined by mapping locations of visual observations and summer mortality sites on 1/20,000 forest cover maps. Aerial telemetry was used to determine summer range locations for deer where visual and mortality locations were not available. Aerial locations were plotted on 1/15,000 airphotos, then transferred onto 1/20,000 forest cover maps to determine location coordinates.

Seasonal Migration Direction and Distance

EXCEL (Microsoft Corporation, Redmond, WA) spreadsheets containing winter and summer locations were used to create two ARCINFO 8.0.2 (Environmental Systems Research Institute, Redlands, CA) coverages, one for each season. Pointdistance command was then used to calculate the distance between the points in the two coverages.   Joinitem and tables commands were used to determine which record in pointdistance output corresponded to the pair of locations for each individual. The resultant table was then exported out of ARCINFO as a dbase IV file, and imported back into EXCEL.

A chi-squared log likelihood test was used to test the null hypothesis that deer migrated in each of eight compass directions equally (Krebs 1999). Manely's alpha was used to determine preference or avoidance of migration routes (Krebs 1999).

Mortality

Mortality signals were usually investigated within 24 hrs of being noted by ground-tracking to the carcass. In a number of instances the carcass was never examined as the radiocollars were returned by hunters who were responsible for the death of the collared deer. Also, in several cases involving deer killed by vehicles, Ministry of Transportation and Highways personnel or Conservation Officers returned collars. Initially, cause of death involving predation was determined from criteria established by O'Gara (1978). These criteria were further refined with information from McNay and Voller (1995) and Roffe et al. (1996). Femur bone marrow consistency was checked as an indication of health at time of death (Cheatum 1949).

Survival Analysis

Program MICROMORT (Heisey and Fuller 1985) was used to calculate daily survival and cause specific mortality rates, seasonally, annually, and across the study period. Annual rates were based on a biological year of June 1st to May 31st (i.e. the survival rate reported for 1988 is for the 365 day period from June 1st 1988 to May 31st 1989). Seasonal survival rates were calculated based on a calendar year with seasons determined by deer movements and behaviour. The four seasons were defined as; Winter (January 1 to April 30) when deer are established on winter ranges, Spring (May 1 to June 30) when deer are migrating to summer and fawning ranges, Summer (July 1 to September 31) when deer are established on summer ranges, and Fall (October 1 to December 31) when deer are in rut and migrating back to winter ranges. Seasonal radiodays and mortalities were pooled across the study period to allow sufficient data for analysis.

Population Modeling

Deer population modeling is somewhat paradoxical. As with any long-lived species, sensitivity analysis reveals that deer population trends are most sensitive to annual variations in adult mortality (see White and Bartmann 1997, for review). However, the greatest annual variability within a population is fawn survival (White and Bartmann 1997, Unsworth et al 1999, but see also Whittaker and Lindzey 1999). Fawn survival in previous deer studies have ranged from 0.10 to 0.78 (Kunkel and Mech 1994, White and Bartmann 1997, Unsworth et al 1999, Ballard et al 1999). Mackie et al. (1998:97) reported whitetail fawn survival ranging from a low average of 0.18 to a high average of 0.68 in several white-tailed populations in Montana. Using maternity rates of road-killed deer and recruitment rates obtained through aerial survey (Kunkel and Mech 1994), Robinson et al. (2002) reported 1999 whitetail fawn survival within the study area as 0.31.

Population growth rates (λ) were estimated with a Leslie Matrix (Leslie 1945) using a female prebreeding model in RAMAS GIS (Akcakaya et al. 1999). Population models were constructed based on a constant maternity rate of 1.83 (Robinson et al. 2002) calculated annual survival rates, and three (high, medium, low) fawn survival rates. High and low fawn survival rates were based on extreme average values reported by Mackie et al (1998:97), 0.61 and 0.18 respectively. Medium fawn survival rate was 0.31, reported by Robinson et al (2002).

RESULTS

Captures

A total of 66 white-tailed deer (63 female, 3 male) were radiocollared and monitored between 1988 and 2001. As all population models are based on female survival and reproduction, the three males captured were not used in any analysis for this report. Any animal that went off the air or died due to collar complication (one female fawn had a front leg entangled in her radio collar when killed by coyotes 84 days after capture), was censored from the data (their surviving radiodays were used although their fates were not). As a result, 63 female white-tailed deer (58 adults and 5 fawns) were monitored amassing 55,343 radio days (Table 1).

Migration

White-tailed deer does in the Pend d'Oreille River valley migrated 360° from their winter range (Figure 3). Only one collared animal was a year round resident of its winter range and one deer emigrated. The average migration distance was 13.3 km straight-line distance (n = 55, σ = 9.73 km, Range 0.85 – 41.7km). Migration directions were not distributed equally in all directions (χ^2 =13.88, d.f. = 7, p = 0.053). North-northeast, and east-northeast directions were preferred, while south-southeast, south-southwest, and west-northwest were avoided (Table 2).

Mortality

Forty white-tailed deer mortalities were investigated from 1988 to 2001, a cause was determined for 33 of these (Table 3). Mortality causes were grouped into 6 categories for analysis (Heisey and Fuller 1985), cougar, hunted, poached, vehicle, natural, and unknown. All predation mortalities were attributed to cougar. Mortalities were classified as natural if the animal died due to poor condition or as the result of an accident.

Annual survival rates ranged from a low of 0.51 in 1995 and a high of 1.0 in 1990. Average annual survival was 0.76 across the study period. Variances associated with calculated annual survival rates vary greatly with sample size (number of radio days), and number of mortalities recorded in a particular year (Table 1). The extremes in variance are demonstrated in the breadth of the confidence intervals surrounding the calculated survival rates (Figure 4).

Cougar predation was the main cause of known whitetail mortalities from 1988-2001, accounting for 12 of 33 mortalities investigated. The cougar mortality rate was highest in 1995 (0.209), and 1999 (0.204). No mortalities were attributed to cougar from 1988 to 1992, and in 1996, 2000, and 2001 (Figure 5, Table 3).

Vehicle accidents were the most constant form of mortality with at least one collared deer killed by a vehicle in 7 of 13 years of study. In total, 8 of 33 known mortalities were attributed to car accidents with the accompanying mortality rate being highest in 1989 (0.196) (Figure 5, Table 3).

Five animals were killed as part of a legal harvest. Although doe permits were issued in every year of the study but 1998 and 1999, all harvest mortalities occurred in 1994, 1995, and 1996. One animal was poached in each of 1989, 1991, 1994, and 2001 (Figure 5, Table 3).

Seasonal Mortality

Seasonal mortality rates were calculated to the end of 2001 and therefore do not include winter 2002 as do the annual survival rates (seasonal rates are based on calendar year January 1 to December 31 where as annual rates are based on biological year June 1 to May 31). Thus seasonal rates show a slightly lower radioday total and one less unknown mortality which occurred in March 2002 (Table 4).

Although fairly constant across seasons, survival was lowest in fall when hunting and poaching accounted for 7 of 10 mortalities. Cougar predation was highest in winter and spring and vehicle accidents were the main cause of summer mortality (Figure 6).

Population Growth Rate and Estimated Density

The use of three fawn survival rates in the population model produced a wide range of finite rates of growth, however, clear trends can be seen. Our model predicts that the white-tailed deer population experienced two periods of increase, and possibly two periods of decreases between 1988 and 2001 (Figure 7). Estimated densities based on the medium population growth model and aerial survey results from 1999 are presented in Figure 8. Our model predicts that the population reached a high in 1992, declined until 1995 and rebounded from 1996 to 2000.

DISCUSSION AND MANAGEMENT IMPLICATIONS

This population of whitetails showed clear preference for migrational routes to the northeast of the Pend d'Oreille, and avoidance of routes to the south and west. These migration routes may likely follow natural movement corridors through the topography. Although deer migrations across large bodies of water have been documented (Boroski et al 1999, Gwilliam personal observation), it would appear that the Pend d'Oreille Reservoir (to the south), and to a larger degree the Columbia River (to the west) provide disincentive to deer migration.

White-tailed deer have been shown to pass migration routes and seasonal ranges along matrinlinial lines (Nelson and Mech 1999). Our capture efforts (focused mainly in the middle and eastern portions of the Pend d'Oreille) may have focused on a few matrilines resulting in our results showing a stronger preference than exists in the population as a whole.

Although both mule deer and white-tailed deer show high fidelity to seasonal home ranges, human induced habitat modifications can cause dramatic alterations in migration pattern. Tierson et al (1985) found that white-tailed deer remained on summer ranges throughout the winter following late fall/early winter logging in adjacent areas. This shift in seasonal habitat use was likely due to the increased foraging opportunities provided by a newly harvested stand. This population of white-tailed deer migrates 360° from the Pend d'Oreille valley, with preferences shown to the north and east. As such, habitat treatment/enhancements targeted for other ungulate species (i.e. mule deer winter range improvements) may in fact be utilized by whitetails that winter in the Pend d'Oreille valley but whose summer migrations take them into or through these improved areas. It does not appear that many deer from the Pend d'Oreille winter range move far enough east to enter endangered caribou habitat along the Salmo-Creston crest.

Because of the small sample sizes and associated large confidence intervals caution should be taken when interpreting survival data from early in the study. With less than ten animals radio collared in 1988 and 1989, little confidence should be placed in the results from those years. Results from the remainder of the study period do, however, offer an interesting look at the population trend of white-tailed deer through the 90's. The predictions of our model are backed by other population indices, collected independently by the MWLAP and Columbia Basin Fish and Wildlife Compensation Program (Figure 9).

Boulanger et al (2000) projected white-tailed deer populations in the Pend d'Oreille valley from 1978 to 1997 based on pellet group counts. Columbia Basin Fish and Wildlife Compensation Program also conducted spotlight counts of deer each spring in the Pend d'Oreille (Gwilliam, unpublished data). These methods produce vastly different absolute numbers making comparison difficult. However, growth rates can be extrapolated from each using the simple formula $\lambda = N_t/N_{t-1}$. We calculated the finite rate of growth projected by each method for each year. These growth rates were then applied to a starting population of 1000 individuals to directly compare each index. Figure 9 shows a direct comparison of the populations projected for each year between 1987 and 2000 by the Leslie matrix model described in this report, Boulanger et al's pellet counts, and Columbia Basin's spotlight counts. Although the end populations vary, all three indices predict that the lowest whitetail populations were likely reached in the mid-nineties. It is believed that tough winters in 90/91 and 92/93 with extended periods of crusted snow, and a heavy doe harvest in 1994 had a strong impact on the deer populations during those years (Gwilliam, unpublished data).

When growth rate is plotted against population density the finite rate of growth declines as the population increases (Figure 10). This is likely due to some density dependent mortality that remains stable or increases at higher densities and denotes some form of density dependent regulation (McCullough 1992).

Our analysis divided mortality causes into six categories, cougar predation, hunting, poaching, vehicle accident, natural mortalities and unknown. Of these six, one would predict that cougar predation and natural mortalities should show density dependence. Hunting may show density dependence if the number of hunting permits and therefore effort is closely tied to deer density. Hunting may show density independence or inverse density dependence if the number of tags issued remains constant while the deer population fluctuates. Although hunter success likely increases with deer density, the total number of deer removed from the population is likely as much a function of the number of permits issued and therefore effort. Both poaching and vehicle accidents could increase with increases in white-tailed deer density. However, poaching opportunities as well as the chance of vehicle accidents rely as much on human behaviour as deer population and are likely both density independent (Lamoureux et al. 2001, Putman 1997). Unknown mortalities are a function of the time the animal is dead before it is detected, and therefore were not analysed further.

Figure 11 shows cause specific mortality rates at varying population densities and a best fit linear trend line for each (it should be noted that these are not significant regressions but merely trend lines and should be interpreted as such). As predicted, cougar and natural mortalities are density dependent (remaining flat or increasing as the population increases). However, hunting appears to be inversely density dependent (the hunting mortality rate increases as the population decreases) likely due to a time lag inherent in the issuance of hunting permits. A goal of the MWLAP in the mid nineties was to stabilize or lower the white-tailed deer population (Woods pers. com.). Our data would suggest that the MWLAP was correct in both its assessments of the population and its management policy. Both poaching and vehicle accidents mortality rates appear to increase as the population declines suggesting that the number of animals killed in these manners may remain constant while the deer population declines.

Traditional theory suggests that cougars subscribe to a land tenure system whereby intraspecific competition for resources limits the population (Hornocker, 1970). Female cougar home ranges are thought to be based on prey availability (Ross and Jalkotzy, 1992), with male home ranges based on female availability. Thus the number of home ranges available to transients sets the cougar population. The idea that cougar populations are limited by social interaction has recently been challenged. Cougars are known to migrate seasonally to follow prey. Seidensticker et al (1973) found that the density of cougars in their study area almost doubled during winter in response to a migrating deer and elk population. By radiocollaring both predator and prey, Pierce et al. (2000) concluded that cougar distributions on a winter range in California were the consequence of prey availability and not land tenure or mutual avoidance. In a second work, Pierce et al. (in press) tracked the numerical (reproductive) response of cougars to a declining mule deer population and found that although displaying an eight year time lag, the cougar population did follow their primary food source lower. Our data suggests that cougar predation on white-tailed deer increases with increased deer density (Figure 11). It would appear that cougar populations, and therefore cougar predation, in the Pend d'Oreille may be directly tied to the number of white-tailed deer. Although the primary cause of cougar mortality in the area is human harvest (Katnik, 2002) and this likely dictates cougar density, an abundant prey base may perennially attract cougars into the valley thus maintaining at least a constant predation pressure.

Natural mortalities for this study were defined as mortalities caused by poor condition. Poor condition could be a result of either short-term food shortages caused by stochastic events such as the harsh winter of 1996/97 or simply due to increased competition caused by an expanding population. It is interesting to note that natural mortalities occurred in the early nineties when the population was predicted to be at its highest, and in 2000 when the population was increasing (Figure 8).

Hunting mortalities were only observed in the mid-nineties when the white-tailed deer population was at its lowest. As the white-tailed deer population was declining, the MWLAP was increasing the number of doe tags issued (Figure 12). The effect of this increased hunting pressure was likely additive to the density dependent natural mortality of the early nineties. In this way the effect of human harvest on the white-tailed deer population may have been multiplied, resulting in the inversely density dependent pattern shown in Figure 11.

RECOMMENDATIONS

The MWLAP has recently returned to the limited use of a doe season for white-tailed deer in part to prevent the whitetail population from expanding. Current whitetail population levels are now close to the levels of 1994 and 1995 (Figure 8). If the current management goal is to maintain low whitetail densities, it would appear that between 390 (1994) and 423 (1995) doe tags should be issued for the entire winter range. This is simply a rough estimate, however, and more precise methods of modeling harvest are available given the known parameters of this population and should likely be explored (see Buckland et al. 2000, and Xie et al. 1999).

Doe seasons have often been used to reduce deer populations, however few replicated experiments that have tested this often used management practice exist. Population modeling suggests that even small increases in the mortality rate of female deer should result in dramatically reduced population growth (White and Bartmann 1997, Robinson unpublished data). Such a shift in harvest regulation provides an excellent opportunity for an adaptive management experiment. This experiment could test the effect of increased doe harvest on both white-tailed deer population growth and sympatric mule deer survival and population growth.

The experiment would involve radiocollaring white-tailed deer in Kootenay Management Unit 4-07 where currently none exist. Mule deer already collared from a past study in addition to a few new collared individuals could be used in both Management Units 4-08 and 4-07. Whitetail doe harvest would be allowed in both units in years one and two. In year three and four, whitetail doe harvest would not be allowed in unit 4-07. This would effectively create six control units where does were harvested (two units in the first two years and one unit in the last two years) and two treatment units where does were not harvested (one unit in the last two years). A repeated measures analysis of variance on survival between treatments and controls would determine if white-tailed deer doe harvest had the desired management effect. It would be predicted that trends in survival and population growth in units 4-07 and 4-08 would be similar in the first two years of the study. Any changes in population trend in years three and four could be attributed to the treatment (cessation of doe harvest).

As mentioned above, increasing white-tailed deer populations are a current management concern. Regulating whitetail populations through habitat modification or reductions in carrying capacity (*K*) are logistically unfeasible due to deer migration and the improbable likelihood of "targeted" habitat treatments. It is unlikely that any habitat modifications designed to either reduce white-tailed deer or increase other ungulate species is likely to be species specific. Limiting whitetail populations through increased doe harvest may be the best management strategy left to managers and should be investigated through modeling or empirical study.

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Table 1. Number of deer radiocollared, radiodays accumulated, and annual survival for each year of study in south-central British Columbia, 1988-2001.

Year	Animals Collared	Radiodays	Mortalities	Annual Survival Rate	Variance
1988	4	724	1	0.6038	0.09279
1989	7	1466	2	0.6076	0.04582
1990	10	2425	0	1.00	0.0
1991	11	3659	1	0.9048	0.00819
1992	15	3934	2	0.8306	0.01188
1993	17	4084	5	0.6395	0.01635
1994	19	4091	4	0.6997	0.01560
1995	21	3823	7	0.5113	0.01680
1996	22	5279	3	0.8126	0.00947
1997	18	5954	2	0.8846	0.00588
1998	23	6491	2	0.8936	0.00505
1999	19	6026	6	0.6945	0.01068
2000	16	3336	3	0.7201	0.01863
2001	17	4051	2	0.8350	0.00113
Span	**63**	**55343**	**40**	**0.7680**	**0.00102**

Table 2. Results of Manly's test of resource selection. A score significantly above or below 0.125 suggests preference or avoidance respectively.

Migration Direction	Use Ratio	Manly's Alpha	Preference or Avoidance
NNE (0°- 45°)	1.455	0.182	Preferred
ENE (46°- 90°)	2.036	0.255	Preferred
ESE (91°- 135°)	1.019	0.127	
SSE (136° - 180°)	0.436	0.055	Avoided
SSW (181° - 225°)	0.436	0.055	Avoided
WSW (226° - 270°)	1.019	0.127	
WNW (271° - 315°)	0.582	0.073	Avoided
NNW (316 - 360°)	1.019	0.127	

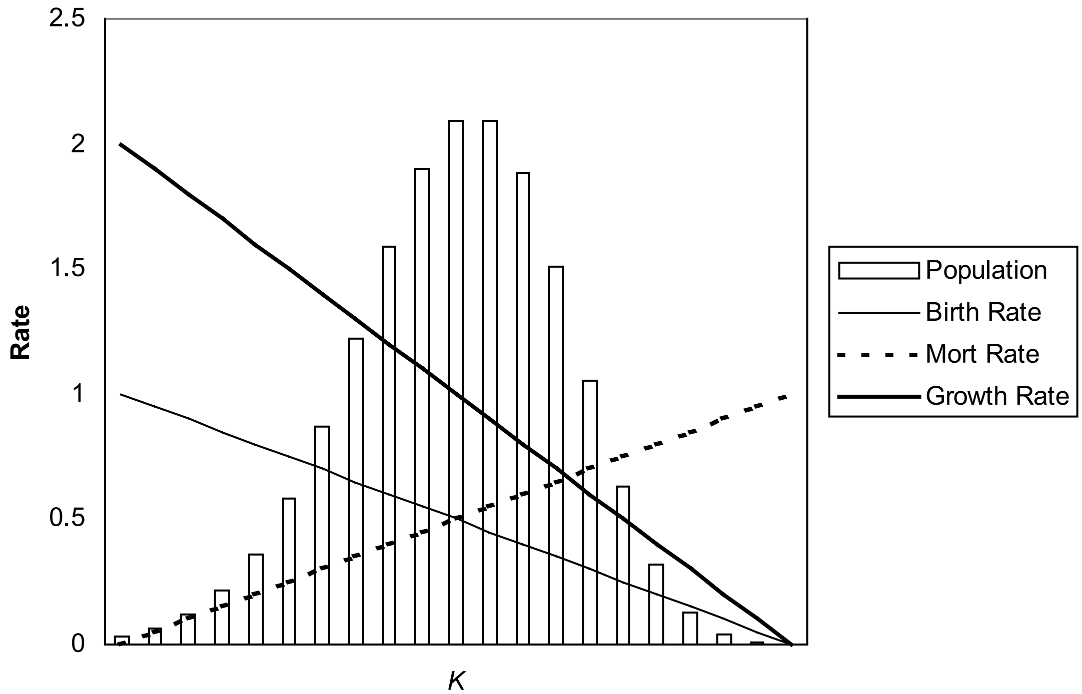
Table 3. Number of mortalities (associated cause specific annual mortality rate), and annual survival rates of female white-tailed deer in the Pend d'Oreille River valley, British Columbia, 1988-2000.

Year	**Cause**						**Total Mortalities**	**Survival Rate**
	Cougar	Hunted	Poached	Vehicle	Natural	Unknown		
1988	0	0	0	0	0	1 (0.39)	1	0.60381
1989	0	0	1 (0.19)	1 (0.19)	0	0	2	0.60756
1990	0	0	0	0	0	0	0	1
1991	0	0	1 (0.09)	0	0	0	1	0.9048
1992	0	0	0	0	2 (0.16)	0	2	0.83059
1993	2 (0.14)	0	0	1 (0.07)	1 (0.07)	1 (0.07)	5	0.63945
1994	1 (0.07)	1 (0.07)	1 (0.07)	1 (0.07)	0	0	4	0.69973
1995	3 (0.20)	2 (0.13)	0	1 (0.06)	0	1 (0.06)	7	0.51131
1996	0	2 (0.12)	0	0	0	1 (0.06)	3	0.81262
1997	1 (0.05)	0	0	0	0	1 (0.05)	2	0.88459
1998	1 (0.05)	0	0	1 (0.05)	0	0	2	0.89361
1999	4 (0.20)	0	0	1 (0.05)	0	1 (0.05)	6	0.69447
2000	0	0	0	2 (0.18)	1 (0.09)	0	3	0.72008
2001	0	0	1 (0.08)	0	0	1 (0.08)	2	0.83506
Total	**12 (0.069)**	**5 (0.028)**	**4 (0.023)**	**8 (0.046)**	**4 (0.023)**	**7 (0.040)**	**40**	**0.76601**

Table 4. Seasonal mortality totals and rates for female white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988–2001.

Mortality Cause	Winter	Spring	Summer	Fall
Cougar	4 (0.0252)	4 (0.0249)	2 (0.0134)	2 (0.0145)
Hunted	0	0	0	5 (0.0364)
Poached	1 (0.0063)	0	1 (0.0067)	2 (0.0242)
Vehicle	2 (0.0126)	2 (0.0124)	4 (0.0268)	0
Natural	2 (0.0126)	2 (0.0124)	0	0
Unknown	0	2 (0.0124)	3 (0.0201)	1 (0.0072)
Radiodays	18461	9495	13259	12155
Survival	**0.94316**	**0.93774**	**0.93294**	**0.92707**

Figure 1. Density dependent birth, mortality, growth rates, and resulting population. Note that as the mortality rate surpasses the birth rate the growth rate decreases below 1.0 (K) and the population declines.



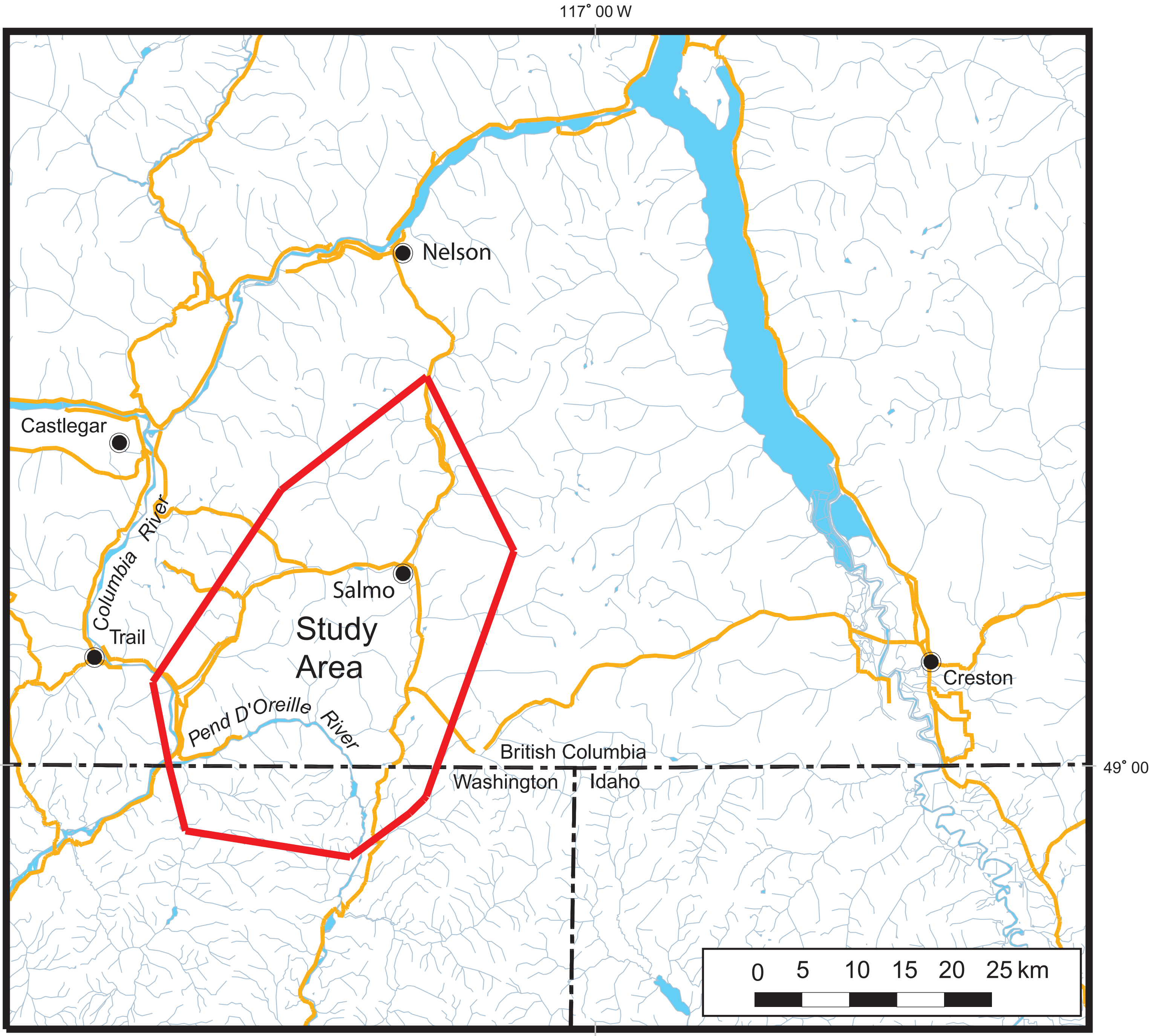


Figure 2. Pend d'Oreille valley white-tailed deer winter range study area.

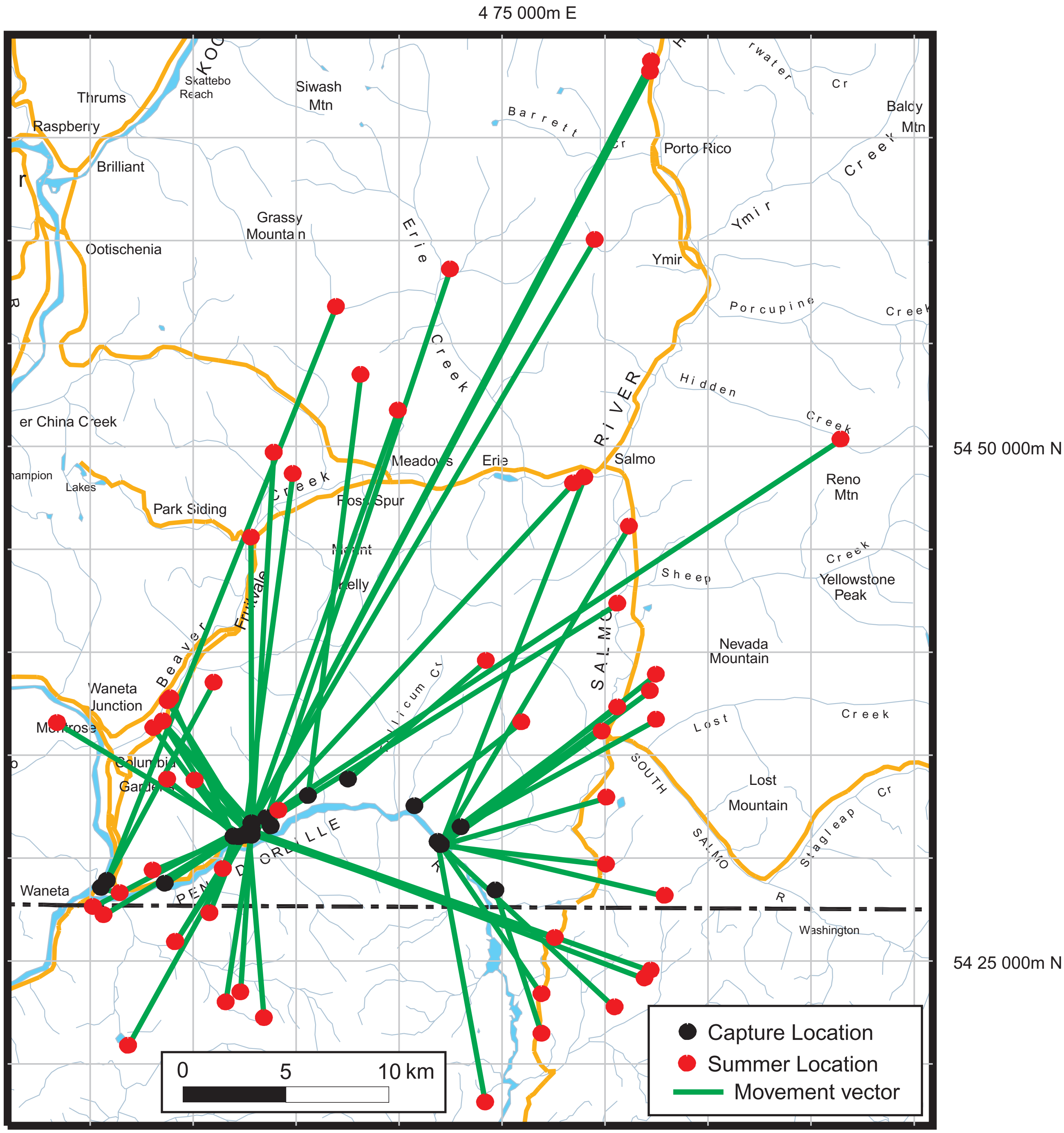


Figure 3. Migration direction and distances of female white-tailed deer in the Pend d'Oreille river valley of British Columbia 1987-2000.

Figure 4. Annual survival rates and associated 95% confidence intervals for white-tailed deer in the Pend d'Oreille river valley 1988 - 2000.

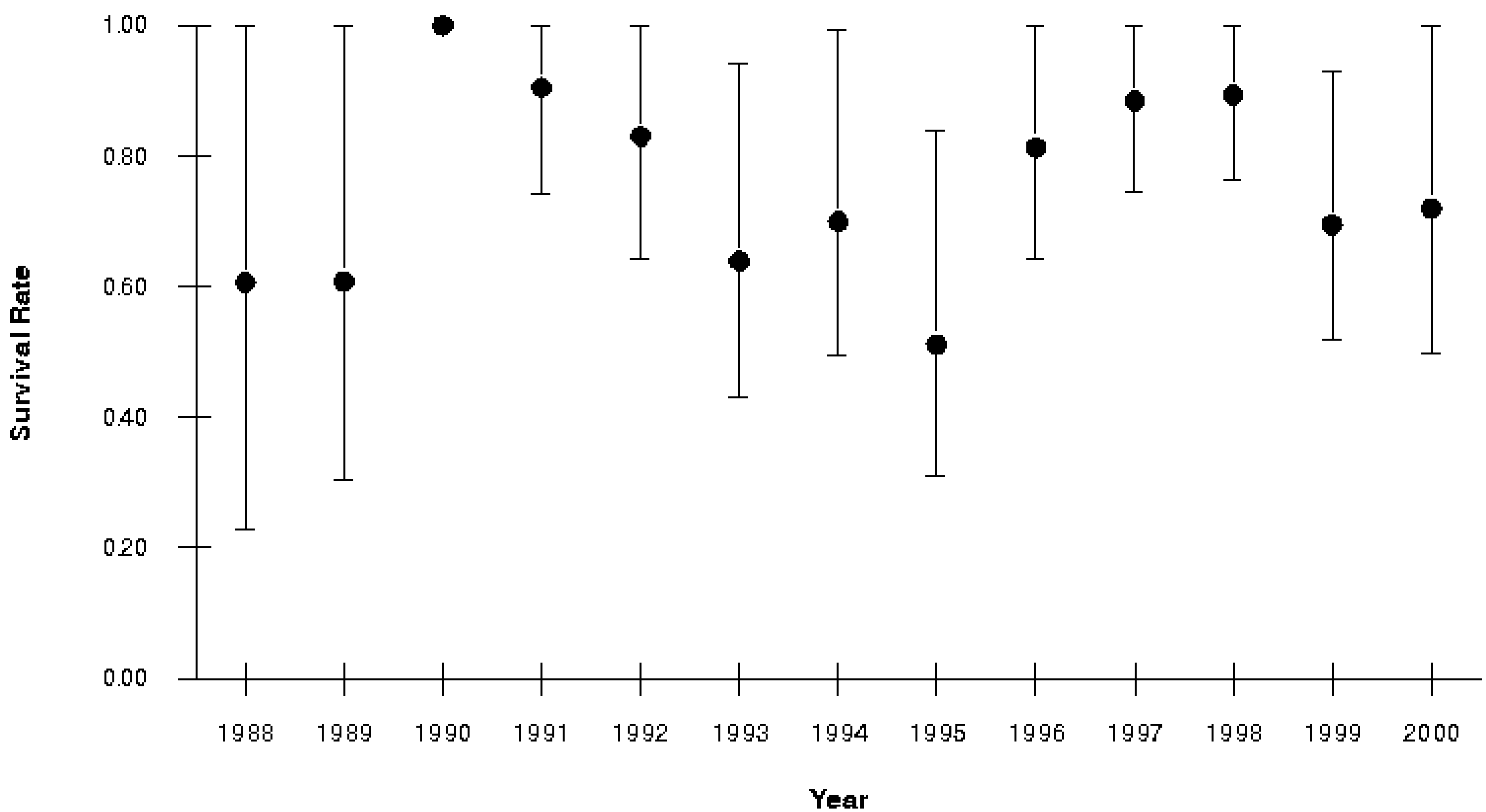


Figure 5. Cause specific mortality rates for female white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988–2000 (note that the x-axis for unknown mortalities had to be increased to fit the 1998 rate).

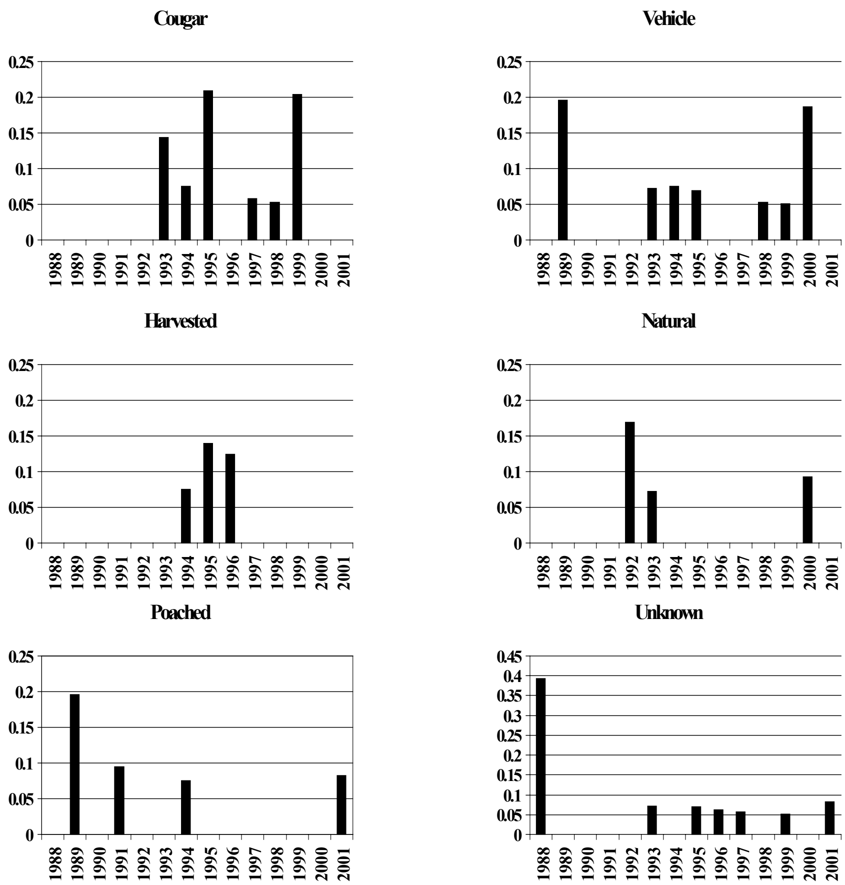


Figure 6. Seasonal cause specific mortality and survival rates for female white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988–2001.

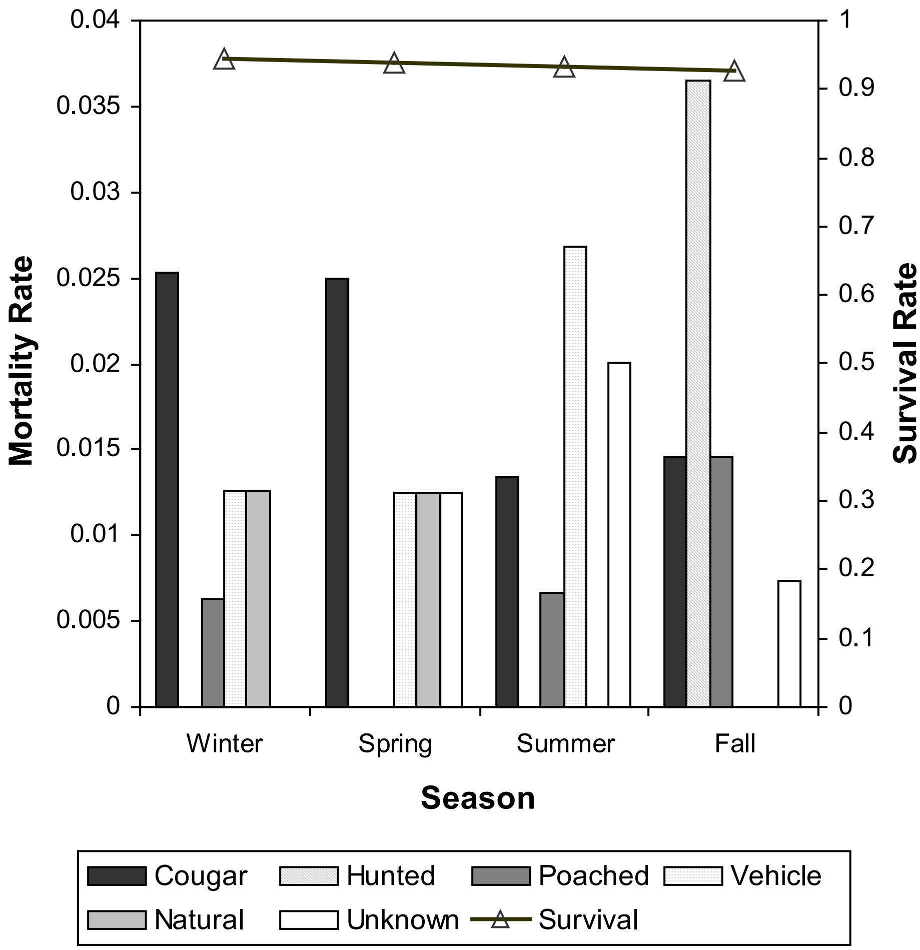


Figure 7. Estimated population growth rates of white-tailed deer in the Pend d'Oreille river valley 1988 – 2000 based on high (0.68), medium (0.31), and low (0.18) fawn survival rates (the solid line marks a stable population level λ = 1.0).

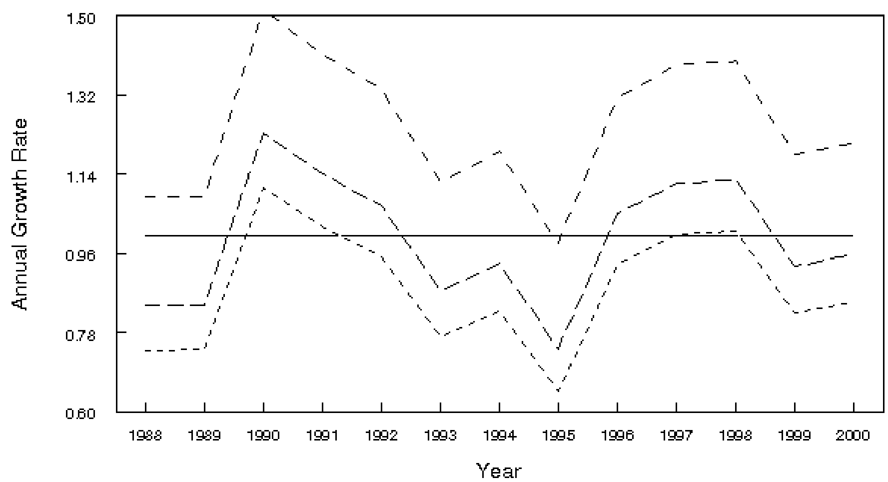


Figure 8. Estimated white-tailed population densities from 1988 to 2001 in the Pend d'Oreille river valley of British Columbia.

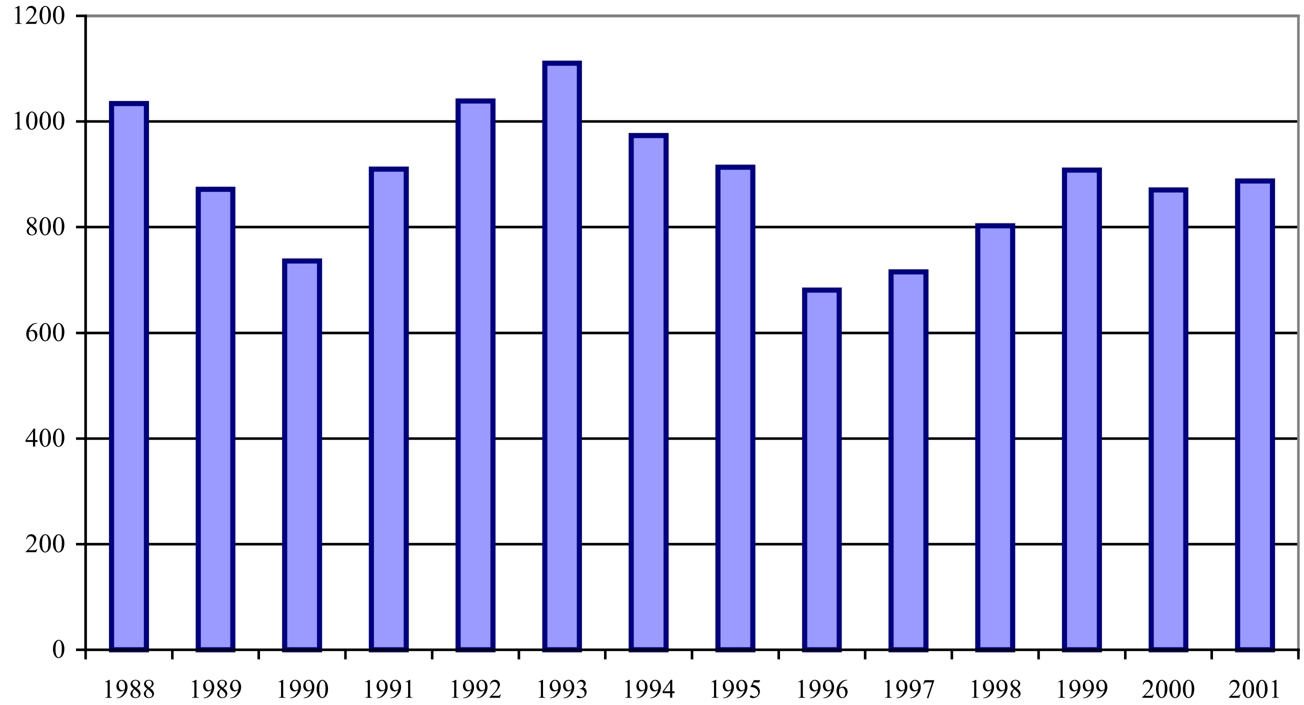


Figure 9. Comparison of three population indicies for white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988 - 2001.

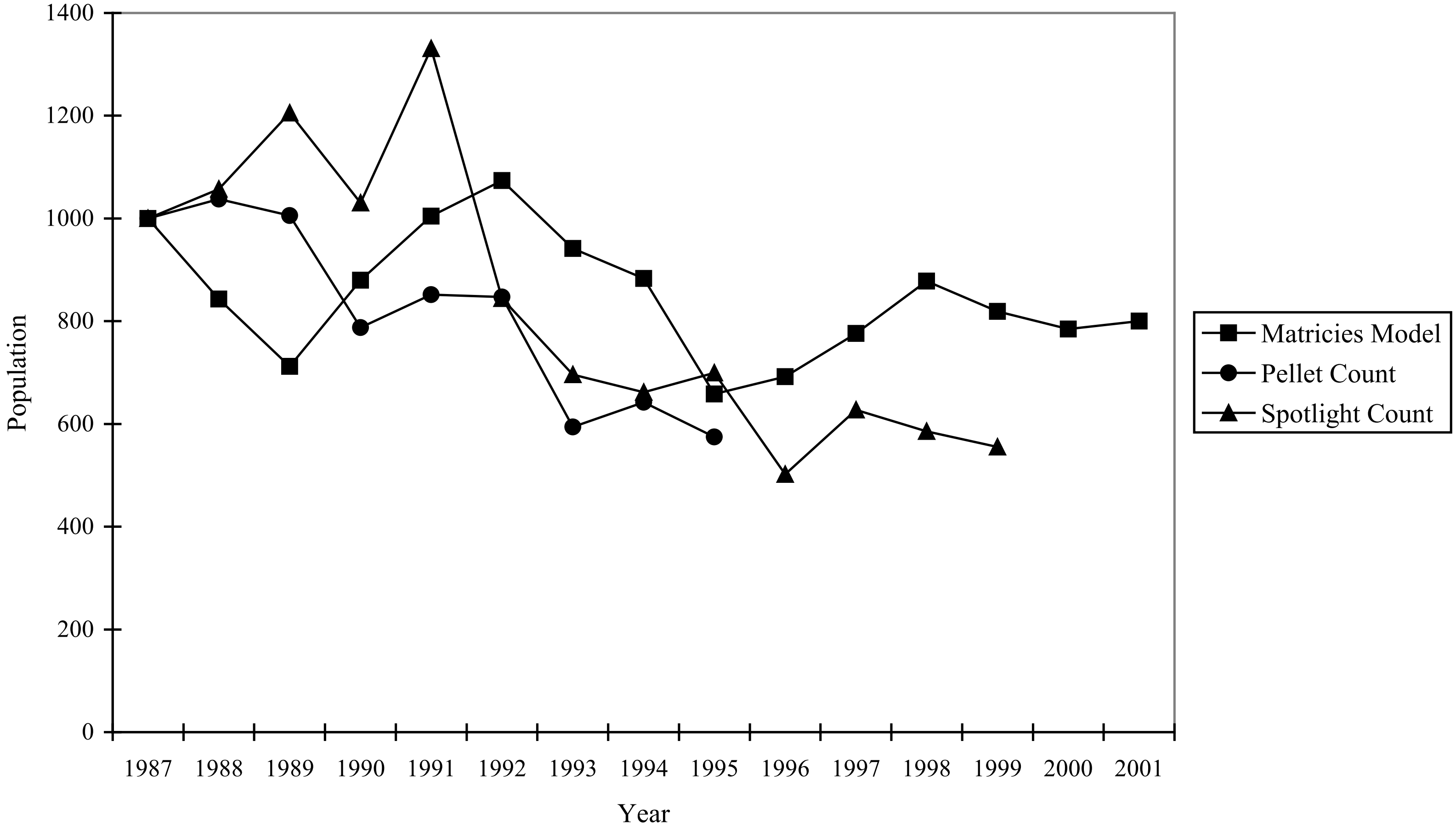


Figure 10. Population growth rate plotted against estimated density of white-tailed deer for the previous year in the Pend d'Oreille river valley of British Columbia 1988 – 2001. The negative slope denotes a slowing growth rate as the population increases and thus density dependence.

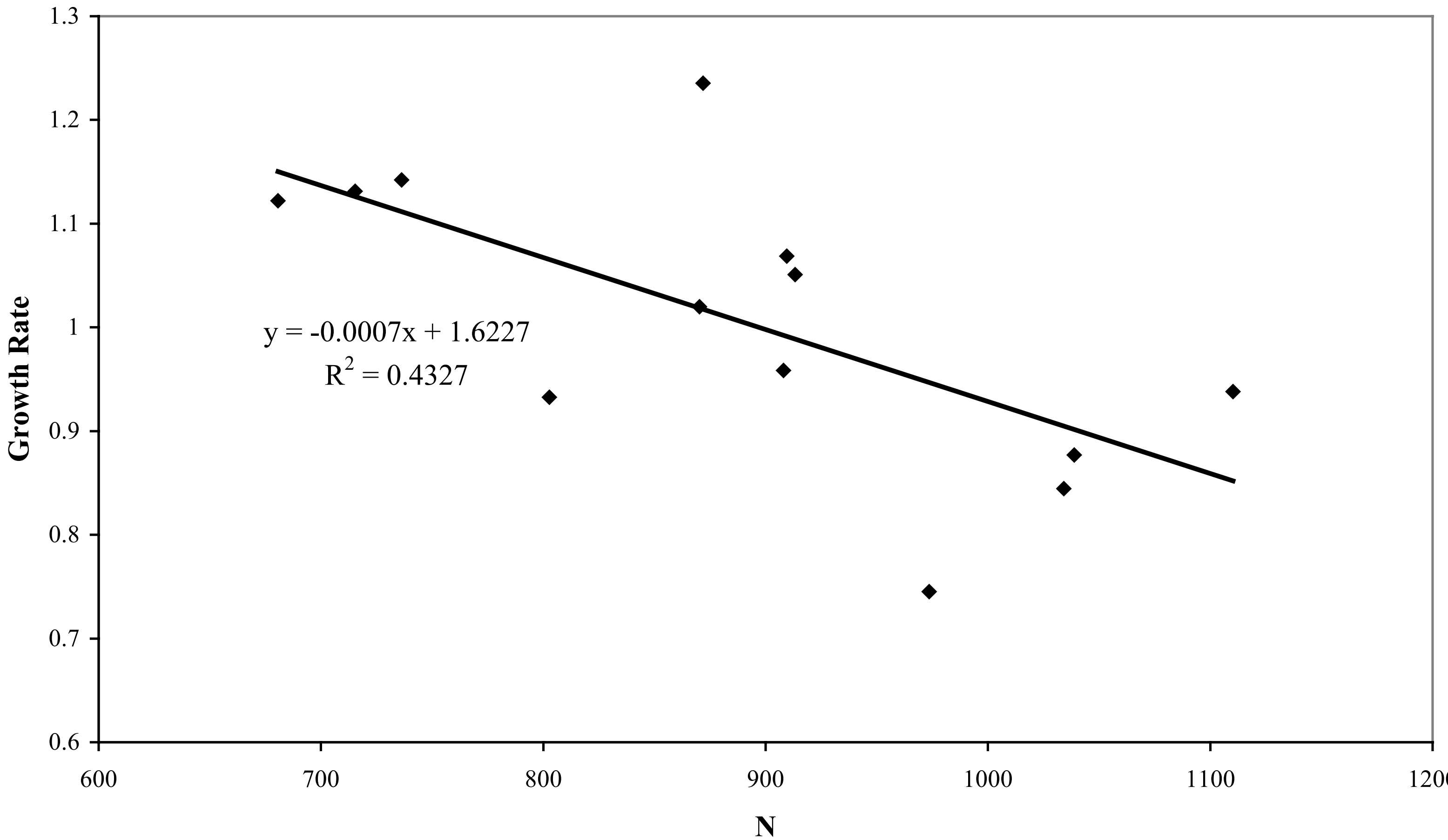


Figure 11. Cause specific mortality rates plotted against estimated population for white-tailed deer in the Pend d'Oreille river valley of British Columbia 1988 – 2000

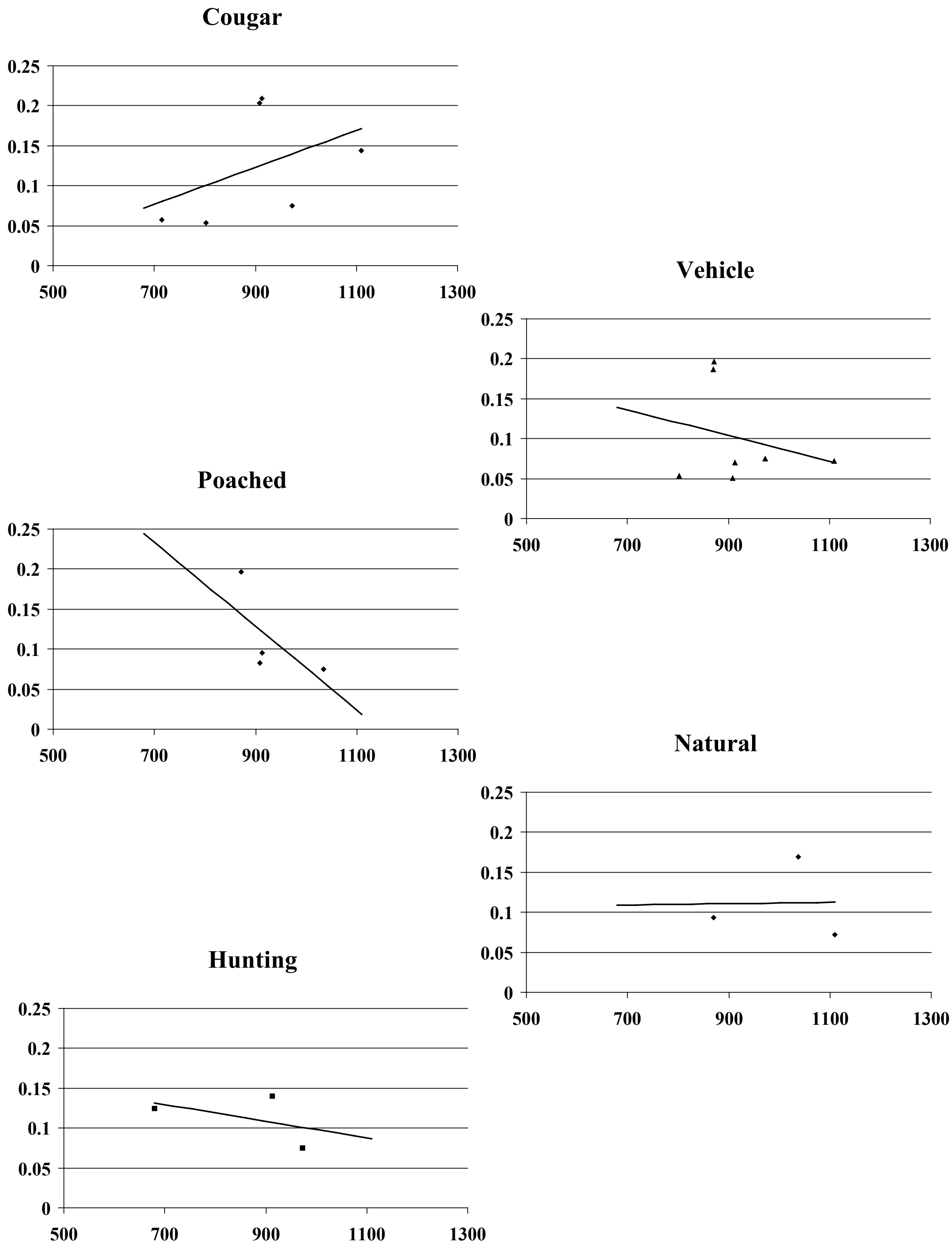


Figure 12. Comparison of white-tailed population, the number of doe tags issued, and the number of does harvested.