



**COLUMBIA BASIN
FISH & WILDLIFE
COMPENSATION
PROGRAM**



**COUGAR PREDATION AND
POPULATION GROWTH OF
SYMPATRIC MULE DEER AND WHITE-
TAILED DEER**

PREPARED BY

Hugh S. Robinson, Robert B. Wielgus, and
John C. Gwilliam

FOR

Columbia Basin Fish & Wildlife Compensation Program

April 2002

Cougar predation and population growth of sympatric mule deer and white-tailed deer.

Hugh S. Robinson^a, Large Carnivore Conservation Lab, Department of Natural Resource Sciences, Washington State University, Pullman WA, 99164-6410, U.S.A.

Robert B. Wielgus, Large Carnivore Conservation Lab, Department of Natural Resource Sciences, Washington State University, Pullman WA, 99164-6410, U.S.A.

John Gwilliam, Columbia Basin Fish & Wildlife Compensation Program, Nelson, BC, V1L 5P5, Canada.

^a Corresponding author.

Current address:

Large Carnivore Conservation Lab

Department of Natural Resource Sciences

Washington State University

Pullman, WA, 99164-6410, U.S.A.

ph. (509) 335-4084

fax (509) 335-7862

email hsrobins@wsunix.wsu.edu

Cougar predation and population growth of sympatric mule deer and white-tailed deer.

Hugh S. Robinson, Robert B. Wielgus, John Gwilliam.

Abstract: Mule deer populations throughout the west are declining whereas white-tailed deer populations are increasing. We compared abundance, fetal rate, recruitment rate, and cause-specific adult (≥ 1 yr. old) mortality rates of sympatric mule and white-tailed deer in south-central British Columbia to assess the population growth of each species. White-tailed deer were three times as abundant (908 ± 152) as mule deer (336 ± 122) (± 1 SE). Fetal rates of white-tailed deer (1.83) were similar to mule deer (1.78) ($t = 0.15$, $df = 13$, $P = 0.44$). There was no difference in recruitment of white-tailed deer (56 fawns:100 does) and mule deer (38 fawns:100 does) ($\chi^2 = 0.91$, $df = 1$, $P = 0.34$). Annual adult white-tailed deer survival ($S_{WT} = 0.81$) was significantly higher ($z = 1.32$, $df = 1$, $P = 0.09$) than mule deer survival ($S_{MD} = 0.72$). The main source of mortality in both populations was cougar predation. The lower survival rate of mule deer could be directly linked to a higher predation rate (0.17) compared to white-tailed deer (0.09) ($z = 1.57$, $df = 1$, $P = 0.06$). The finite growth rate (λ) of mule deer was 0.88 and 1.02 for white-tailed deer. We suggest that the disparate survival and predation rates are caused by apparent competition between the two deer species.

Introduction

Mule deer (*Odocoileus hemionus*) populations are believed to be decreasing while white-tailed deer (*O. virginianus*) are increasing throughout North America (Gill 1999). In a recent survey, 45% of the jurisdictions polled reported decreasing populations of mule deer (Crete and Daigle 1999). By contrast, only 13% reported decreasing white-tailed deer, whereas most (52%) reported increasing populations of whitetails. The reason for concurrent declines in mule deer and increases in white-tailed deer remains unclear. Indirect and direct competition for resources between the two species does not appear significant. For instance, Anthony and Smith (1977) and Swenson et al. (1983) described habitat segregation between the species, even when populations were allopatric. As such, habitat segregation usually prevents direct competition. When direct competition between deer species does occur, mule deer appear dominant (Anthony and Smith 1977, Wood et al. 1989).

It has been suggested that quality and availability of mule deer habitat has declined because of timber harvest, changes in fire regime, and direct competition with livestock and larger ungulates, namely elk (Anthony and Smith 1977, McNay and Voller 1995, Clements and Young 1997, Gill 1999). Conversely, white-tailed deer habitat quality may have increased in response to human agricultural practices (Swenson et al. 1983, Roseberry and Woolf 1998). Others have suggested stochastic events (e.g., severe winter, drought) (Unsworth et al. 1999), hunting (McCorquodale 1999), and predation (Hatter and Janz 1994, Ballard et al. 2001), as capable of causing mule deer declines.

However, it is unclear why any of these latter pressures would affect mule deer more than sympatric white-tailed deer.

In 1996, extreme snowfall (Figure 1) reduced densities of both white-tailed deer and mule deer in southern British Columbia. Following this harsh winter, the white-tailed population was believed to recover quickly whereas the mule deer population appeared to continue to decline (G. Woods, British Columbia Ministry of Environment Lands and Parks, Nelson, B.C. pers. com.). We conducted a retrospective, mensurative experiment (Eberhardt and Thomas 1991) to test whether these perceived trends were real, and if so, to test 4 hypotheses that could help explain the observed population trends.

The factors that are thought to limit ungulate species can be grouped into four categories: 1) human harvest (Caughley and Sinclair 1994:286); 2) stochastic events that are density independent (Unsworth et al. 1999); 3) food and habitat limitation, which are density dependent if habitat quality is stable (McCullough et al. 1990; Mackie et al. 1998); and 4) predation, which is density dependent in a single predator/single prey system, and density independent and possibly inversely density dependent in multi-prey systems (Messier 1994). Predation is often the leading cause of adult mortality in deer populations (see example Bleich and Taylor 1998) and thus may have the most dramatic effect on population growth (White and Bartmann 1997).

The primary purpose of this research was to determine the population trend of both deer species, and if any difference in growth rate existed, to identify the most likely cause of the divergence. We tested 4 plausible hypotheses to assess which factor(s) were most limiting the mule deer populations in south-central British Columbia: 1) over hunting; 2) environmental stochastic effects; 3) resource limitation or poor habitat; and 4)

predation. A secondary purpose was to determine if predation on mule deer was consistent with density dependent or density independent population processes.

The hunting hypothesis predicts that any observed decline in mule deer is caused by human-caused mortality. If excessive hunting is causing mule deer populations to decline, most adult mortalities should be attributed to hunter harvest. Furthermore, adult female mule deer should show higher rates of human caused mortality than adult female white-tailed deer.

The stochastic event hypothesis predicts that both species are limited by random, density independent events that reduce maternity, recruitment, and survival. Both white-tailed deer and mule deer should be susceptible to such events and therefore both species should show similar directional trends in their vital rates over time. Mule deer mortality should be positively correlated with white-tailed deer mortality among years. Any differences in growth rate should be caused by proportional (not directional) differences in effect of environment on vital rates (e.g., reproduction, natural mortality). If stochastic events affect mule deer more dramatically than white-tailed deer, the correlation between mule deer survival winter severity should be greater than for white-tailed deer.

The food/habitat hypothesis predicts that forage is limiting the mule deer population by reducing maternity, recruitment, and survival. If both species are limited by habitat (e.g., through limitation in food resources), population growth rates should parallel one another, with growth slowing as the populations tend toward carrying capacity (McCullough 1992). If mule deer are more limited by habitat (through intraspecific competition and/or interspecific competition with white-tailed deer), overwinter survival should be lower than for whitetails, with most winter mortalities

caused by malnutrition (Short 1981). Furthermore, maternity and recruitment levels should also be lower for mule deer because of poor female condition (Connolly 1981:247).

The predation hypothesis predicts that differences in population growth are caused by differences in predation rate. If predation is limiting, it should be the primary cause of adult mule deer mortality. Maternity should be high whereas recruitment should be low. Following the severe population reductions in the winter of 1996/97, both species of deer should have been at low densities relative to normal local levels. Messier (1994) showed that type III, density dependent predation was especially strong at lower ranges of prey density. The density dependent predation hypothesis predicts that as the mule deer population declines, the predation rate will decline because of a decrease in the predator functional response (the number of kills per predator per unit time) and numerical response (the number of predators per unit area) (Solomon 1949; Messier 1994). White-tailed deer and mule deer growth rates should parallel one another with predation rates decreasing with decreased prey densities. The density independent predation or apparent competition hypothesis (Holt 1977) predicts that the mule deer mortality rate will remain high (type I total predation rate) and/or increase (type II total predation rate) as the mule deer population declines because of the presence of alternate prey (white-tailed deer) (Messier 1994; Sinclair and Pech 1996).

Study area

Our study area was located in south central British Columbia between the towns of Creston (49°06N, 116°31W) and Castlegar (49°18N, 117°38W) (Figure 2). It encompassed approximately 4000 km² in south central British Columbia, including the headwaters of the South Salmo, and Upper Priest rivers, and the confluence of the Pend d'Oreille and Columbia Rivers. The physiography of the area is mountainous with elevations ranging from 450 m to 2,165 m.

The climate is Pacific Maritime / Continental with the majority of annual precipitation falling in the form of snow (Environment Canada, Vancouver British Columbia). Environment Canada maintains weather stations on the east (Creston) and western (Castlegar) edges of the study area and provided the following data. Mean (1961 to 1990) temperatures range from -3.0 C° (January) to 19.3 C° (July) in Creston, and from -3.2 C° (January) to 19.9 C° (July) in Castlegar. Mean (1961 to 1990) annual snowfall is 140.6 cm in Creston (el. 597 m) and 224.6 cm in Castlegar (el. 494 m).

The study area is within two biogeoclimatic zones; the interior cedar - hemlock (ICH), and the Engelmann spruce – subalpine fir (ESSF) (Meidinger and Pojar 1991). The ICH zone extends from the lowest elevations of the study area to approximately 1,200m. Western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are the dominant tree species in mature forests, with black cottonwood (*Populus balsamifera trichocarpa*) the climax in more moist areas. Open mixed stands of Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) are common on more xeric, south facing slopes (Ketcheson et al. 1991). The ESSF zone occurs from

approximately 1,200 m to 2,100 m. White spruce (*Picea glauca*) dominates the climax forest, with subalpine fir (*Abies lasiocarpa*) composing the understory, and lodgepole pine (*Pinus contorta*) common following fire (Coupe et al. 1991).

Fire suppression in the last 50 years has halted the main source of natural disturbance. The last major fires in the area occurred in the 1930s and have now regenerated to mixed coniferous stands (Woods 1984). Timber has been harvested in the area since the turn of the century, and forestry is now the dominant form of disturbance.

The combination of climate and physiography combine to create seasonally migratory deer populations (e.g., Garrott et al. 1987). Both white-tailed deer and mule deer congregate on winter ranges between December and April. Deer winter ranges are generally on south to west facing slopes and provide juxtaposition of open shrub fields and timber stands with higher canopy closure (Woods 1984; Pauley et al. 1993; Armleder et al. 1994). Higher elevation winter ranges (i.e., 900-1,200 m) are almost exclusively occupied by mule deer, whereas lower elevation ranges (i.e., ≤ 900 m) are predominantly used by white-tailed deer. Most winter ranges are located wholly within the ICH zone. Both species range higher into the ESSF during summer with mule deer averaging maximum elevations of 1,800 m in early October. White-tailed deer do not range as high in elevation, but have been observed up to 1,700 m (J. Gwilliam and H. Robinson, unpublished data).

In addition to deer; elk (*Cervus elaphus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and mountain caribou (*Rangifer tarandus caribou*), were found in the study area, roughly in that order of abundance. Common predators included coyotes (*Canis latrans*), black bears (*Ursus americanus*), bobcats (*Lynx rufus*), and cougars

(*Puma concolor*). Low numbers of grizzly bears (*Ursus arctos*), lynx (*Lynx canadensis*), and wolves (*Canis lupus*) were also present over the course of the study.

Methods

Trapping and monitoring

The Columbia Basin Fish and Wildlife Compensation Program began radio collaring and monitoring deer in February 1997. Both mule and white-tailed deer were added to the sample each winter in an attempt to maintain a sufficient sample size of 40-50 animals of each species (Pollock et al. 1989). Deer were captured on winter ranges (Figure 3) using helicopter net gunning and Clover traps from December to March. Additional animals were chemically immobilized opportunistically over the summer months. Animals were injected with a mixture of 4 mg/kg Telazol™ (tiletamine/zolazepam) and 2 mg/kg Rompun™ (xylazine hydrochloride) using radiotelemetry darts (Pneu-Dart Inc. Williamsport, Pennsylvania) (Kilpatrick et al. 1997). Each animal was fitted with a radio transmitter equipped with mortality switch on a 6-hr delay (Lotek Inc., Newmarket, Ontario, Canada). Through a combination of aerial and ground telemetry, deer were checked for mortality signals daily during spring and summer. Frequency of monitoring was reduced in winter to every two or three days because of reductions in staff, and the reduced risk of carcasses being scavenged in the absence of bears. Any deer that died within 7 days of handling was censored from the database. All animals were handled in accordance with Washington State University Animal Care Permit #2843.

Adult mortality

Mortality signals were normally investigated within 24 hrs of first receiving a mortality signal. Cause of death was established based on carcass condition. For example, McNay and Voller (1995) classified fresh kills with neck and head injuries, clean incisions at the gut, and partially buried remains as predation by cougars (see also O’Gara, 1978; Roffe et al., 1996). Bone marrow consistency was checked as an indication of health at time of death (Cheatum 1949).

Program MICROMORT (Heisey and Fuller 1985) was used to calculate survival and cause specific mortality rates, both within years and across the study period. To have sufficient data to analyse seasonal survival, we pooled seasonal data across all four years of the study. Seasons were divided into summer (July 1 to Sept 20), fall migration/rut (Oct 1 to Dec 31), winter (Jan 1 to April 30) and spring migration (May 1 to June 30) based on the movement patterns of radio-collared mule deer (e.g., see Garrot et al. 1987). One tailed binomial Z tests were used to test the null hypothesis that mule deer mortality was less than, or equal to (\leq) white-tailed deer mortality rates (Zar 1984:101; Nelson and Mech 1986). A simple regression was used to test for correlation between annual adult survival rates of the two species. A higher human-caused mortality rate for mule deer would support the over-hunting hypothesis. A higher natural mortality rate for mule deer would support the stochastic event and/or food/habitat hypotheses. A higher predator-caused mortality rate for mule deer would support the predation hypothesis.

Reproduction and maternity

Road-killed does were examined for fetuses prior to parturition (June 1) to determine maternity (*mx*) rates. Fawn mortality was calculated using the difference between maternity rates and spring fawn/doe ratios acquired from aerial survey (Kunkel and Mech 1994). A *t*-test assuming equal variances was used to test for differences in maternity rates. Maternity is considered an indication of doe health and therefore habitat quality. Lower maternity in mule deer would suggest that they were disadvantaged because of poor habitat quality supporting the food/habitat hypothesis.

Abundance and recruitment

We determined sex and age ratios, as well as population and recruitment estimates using aerial surveys of designated winter ranges containing radio-collared deer (Bowden et al. 1984; Samuel et al. 1992; Unsworth et al. 1994) (Figure 3). Fawns were considered recruits at 9 months of age (only after being exposed to mortality factors similar to those of adults) (Bergerud and Elliot 1986). Overwinter survival of deer is often low, and in several studies fawn mortality has been shown to be as great as 90% before November (Kunkel and Mech 1994). Therefore, the aerial survey was conducted in late winter, before antler drop but late enough to allow an accurate measure of recruitment.

Winter ranges were stratified into three qualitative categories (high, medium, low) based on an existing inventory (Heaven et al. 1998), a priori knowledge, and expected deer densities. A random sample of each strata was surveyed from 12-14 February, 2000 (Unsworth et al. 1994). Deer were classified as recruits/yearlings, adult does, and adult bucks based on body size and presence or absence of antlers. Count data, group size,

habitat type, and activity of the deer when first spotted (resting, standing, running) were then analysed using program AERIAL SURVEY (Unsworth et al. 1994) to calculate fawn:doe ratios and abundance of each species. AERIAL SURVEY uses sightability models (Samuel et al. 1987) developed for elk, mule deer, bighorn sheep, and moose. For our analysis we used the mule deer, Hiller 12-E, Idaho (winter) model. Difference in recruitment was tested using the chi-squared test of homogeneity (Sauer and Williams 1989; Unsworth et al. 1994). Low recruitment in both species would support the density dependent predation hypothesis. Significantly lower mule deer recruitment (with similar maternity rates) would support the density independent predation hypothesis.

Population growth

Population growth rates (λ) were estimated with a Leslie Matrix (Leslie 1945) using a female pre-breeding model in RAMAS GIS (Akçakaya et al. 1999). In a pre-breeding model, the earliest age class in the matrix is almost 1-yr-olds (Akçakaya et al. 1999:138). Fecundity rates were one half (female only) the recruitment rate. Fecundity of one year olds was assumed to be half that observed in adults, as this would be their first breeding season (Carpenter 1997; Mackie et al. 1998:95). We assumed, because of limitations in age specific maternity and survival rates, that all 2+ year old females had the same fecundity and survival rates. Adult female survival was calculated using program MICROMORT by censoring all males from the data set. For both white-tailed deer and mule deer, maximum age was set at 13yrs. A sensitivity analysis was conducted on each age-class model to determine which vital rate, fecundity or survival, had the greatest effect on the population's finite rate of growth (Akçakaya et al. 1999:56). Mean

geometric (span) and annual growth rates were calculated for each year based on the method above.

Density

We estimated density, or relative number (N), for each species in each year of the study (1997-2000) by solving for N_{t-1} using the equation: $R_t = N_t/N_{t-1}$. Where, R is the annual growth rate, and N_t is the population estimated from the 2000 aerial survey.

Density dependent vs. density independent predation

We tested for density dependent, and density independent predation by plotting predation rate against estimated prey density or relative abundance. The density dependent predation hypothesis predicts that predation rate will increase with increasing prey density. The density independent, or inversely density dependent, predation hypothesis predicts that the predation rate will remain steady or increase with decreasing prey density (Messier 1994).

Results

Trapping success and sample size

From March 1997 – 2000, 43 mule deer and 27 white-tailed deer were radio collared and monitored. The total number of animals, and radio days for each year of study are given in Table 1.

Adult mortality

Twenty-one mule deer mortalities were investigated. Causes of mortality were divided into 5 categories for this analysis (Heisey and Fuller, 1985): cougar, other predation (including one bobcat and one unknown predation), natural (both mortalities were caused by malnutrition/poor condition), vehicle, and unknown (Table 2). No mortalities were attributed to hunting.

Thirteen white-tailed deer mortalities were investigated. As with mule deer, causes of mortality were grouped into 5 categories for this analysis (Heisey and Fuller 1985): cougar, other predation, natural (one accidental injury of a hind leg that we believe led to poor condition and eventually death), vehicle, and unknown (Table 3). No white-tailed deer mortalities were attributed to poor condition/malnutrition. Like mule deer, no collared white-tailed deer were harvested during the study.

Annual survival of mule deer ($S_{1997} = 0.62$ and $S_{1998} = 0.68$) was lower than white-tailed deer survival ($S_{1997} = 0.89$ and $S_{1998} = 0.94$) during the first two years of study ($z_{1997} = 1.88$, $df = 1$, $P_{1997} = 0.03$ and $z_{1998} = 2.02$, $df = 1$, $P_{1998} = 0.02$). In the last two years of the study, white-tailed deer survival decreased ($S_{1999} = 0.77$ and $S_{2000} = 0.63$), whereas mule deer survival steadily increased ($S_{1999} = 0.72$ and $S_{2000} = 0.83$), thus there was no

difference in mortality in 1999 ($z_{1999} = 0.35$, $df = 1$, $P_{1999} = 0.36$), and mule deer survival was actually higher in 2000 ($z_{2000} = 1.30$, $df = 1$, $P_{2000} = 0.09$) (Figure 4). Over the course of the study, annual adult mule deer survival ($S_{Span} = 0.72$) was significantly lower than annual white-tailed deer survival ($S_{Span} = 0.81$) ($z_{Span} = 1.32$, $df = 1$, $P_{Span} = 0.09$) (Figure 4), and there was a negative correlation ($R = -0.89$, $R^2 = 0.79$, $p = 0.11$) between the two. The significant difference in survival rates, and perhaps more importantly their negative correlation over time, suggests that stochastic events are not the cause of mule deer decline.

Seasonal mule deer survival was lowest during winter ($S = 0.89$), whereas white-tailed deer survival was lowest in spring ($S = 0.93$) (Figure 5). Cougar predation was the dominant cause of mule deer mortality in all seasons except fall, when only unknown mortalities were recorded. Cougar predation was also the dominant cause of white-tailed deer mortalities in all seasons except summer, when all mortalities recorded were classified as either vehicle or unknown. The food/habitat hypothesis predicted that mule deer mortality would be highest in winter, but that malnutrition/natural causes should be the chief source of mortality. Although mule deer survival was lowest in winter, cougar predation was the main cause of mortality, not malnutrition. Thus, the food/habitat hypothesis does not seem to be supported by the adult mortality data.

Determining cause-specific mortality relies on gaining quick access to the carcass, before scavengers have removed all evidence that may help determine the cause of death. Unfortunately, this was not always possible, thus 4 mule deer and 2 white-tailed deer had to be classified as unknown mortalities. We analysed these data two ways; first by censoring unknown mortalities completely from the data set. This results in higher

overall survival rates and slightly lower variances (Table 4) and showed that mule deer suffered from significantly higher other predation ($z = 1.42$, $df = 1$, $P = 0.08$) than did white-tailed deer. Based on these data, we divided all mortalities into just two categories, predation (including cougar) and other, (unknown mortalities were simply grouped in with all other mortalities). This more conservative analysis also showed that mule deer suffered from significantly higher predation ($z = 1.57$, $df = 1$, $P = 0.06$) (Table 5).

Maternity

Road-killed mule deer were checked for fetuses from 1997 to spring 2000. White-tailed road-killed deer were only examined during spring 2000. All adult deer contained fetuses. There was no difference in fetal rates between mule deer ($\mu = 1.78$, $SE = 0.22$, $n = 9$) and white-tailed deer ($\mu = 1.83$, $SE = 0.31$, $n = 6$) ($t = 0.15$, $df = 13$, $P = 0.44$). The similarity in fetal rates suggests that mule deer does are not in poorer condition than white-tailed does, and are therefore not disadvantaged by poorer habitat due to intraspecific or interspecific competition, or otherwise denuded habitat quality.

Abundance and recruitment.

An aerial survey conducted in February 2000 showed that white-tailed deer were almost three times as abundant (908 ± 152) as mule deer (336 ± 122) within the study area ($\pm 1SE$). White-tailed deer recruitment (56 fawns:100 does) was higher than mule deer (38 fawns:100 does), although not significantly so ($\chi^2 = 0.9050$, $df = 1$, $p=0.34$). These relatively low recruitment rates suggest that fawns of both species may suffer high predation or other unknown mortality during their first year of life.

We observed fawn:doe ratios of 38:100 mule deer, and 56:100 white-tailed deer. Based on these recruitment rates and the prepartum maternity rates discussed above, we estimated fawn survival of 0.21 for mule deer, and 0.31 for white-tailed deer.

Population growth

Using fawn recruitment rates from 2000 and annual adult survival rates from each year, we estimated annual growth rates (R) and mean annual geometric growth rate (λ) for each species over the course of the study. Assuming fawn survival did not vary significantly from 2000, white-tailed deer showed high growth following the hard winter of 1996, with growth slowing significantly in 1999 and the population declining in 2000 (Figure 6). Mule deer showed a lower initial growth rate that steadily increased to a positive growth level in 2000 (Figure 6). However, based on this model over the course of the study, mule deer decreased annually by 12% ($\lambda = 0.88$), while the white-tailed deer population increased annually by 2% ($\lambda = 1.02$), with whitetail growth in 1996 and 1997 countered by declines in 1999 and 2000. Both populations were most sensitive to changes in adult survival, with the elasticity for adult survival (0.83) much higher than for fecundity (0.17).

Density dependent vs. density independent predation

We plotted total predation rates against population densities estimated through the method discussed above (Figure 7). Predation rate seemed to increase with increasing prey density (density dependent) for white-tailed deer. By contrast, predation rate

seemed to increase (inversely density dependent) with decreasing prey density of mule deer.

DISCUSSION

The main cause of adult mortality for both species of deer was cougar predation. However, predation was significantly higher for mule deer than for white-tailed deer. White-tailed deer were three times as abundant as mule deer within the study area, but there were no differences in maternity and recruitment rates. Our results indicate that white-tailed deer had a considerably higher ($\lambda = 1.02$) geometric mean growth rate than mule deer ($\lambda = 0.88$) over the course of the study. The difference in population growth between mule deer and white-tailed deer appears to be caused by predation in general and cougar predation in particular.

Hunting hypothesis

If human harvest was responsible for the decline of mule deer in the study area, female mule deer should have suffered higher harvest rates than white-tailed deer. Humans during the course of this study killed no radio collared deer of either species. However from 1997 to 1999, 96 mule deer and 312 white-tailed deer were harvested from management units 4-7 and 4-8, which make up our study area (British Columbia Ministry of Environment Lands and Parks, Cranbrook B.C., unpublished data). This apparent discrepancy in our results may be a factor of the small number of males radio

collared (Table 1). Given that white-tailed deer were found to be 3 times as abundant as mule deer, harvest rates seem to be in proportion to each species' availability. Human harvest does not seem to account for the difference in growth rate or population size of these two species.

Stochastic event hypothesis

Several researchers have documented high mortality rates as a result of particularly harsh winters (Loison and Langvatn 1998; McCorquodale 1999). If both species were affected by stochastic events, there should be no significant directional difference in the trends of their annual survival rates over time. Unsworth et al. (1999) saw a strong correlation in survival rates of mule deer across three states, and suggested that stochastic events may regulate deer populations by having a strong influence on fawn recruitment. In our study area however, there were significant differences in adult survival in the first two and last year of the study, and across the entire study period when all mortalities were pooled (Figure 4). A comparison between the survival rates of both species (Figure 4) also shows a negative correlation between the two ($R = -0.89$). Finally, the differences in survival were not caused by differences in mortalities attributable to malnutrition or starvation, suggesting that environmental stochastic events are not responsible for declines in this mule deer population.

Food/habitat hypothesis

All mammalian females, including deer, must reach some level of body fat before they are able to ovulate and conceive (Connolly 1981:247). Obtaining this level of body

fat is especially difficult for yearling females that are still growing (Carpenter 1997), hence fecundity levels in young deer are normally lower than in adults (Mackie et al. 1998:95). Although our sample of fetal rates was very small, the numbers found are very similar to rates reported by earlier studies in the same region. Just south of our study area, Zender (1987) found 1.74 fetuses per pregnant road-killed white-tailed deer ($n = 106$) compared to 1.83 in this study. Zeigler (1978) sampled 61 mule deer in Central Washington and counted 1.73 fetuses per doe, compared to 1.78 in our area. High degrees of variation are often seen in both species and are likely tied to differences in predominant habitat type. For example, Mackie et al. (1998:94) found the lowest fetal rates in mountain-foothill environments. The habitats studied by Zender (1987) and Zeigler (1978) are very similar to our own and are likely typical of animals inhabiting this environment, suggesting that the maternity rates we found were representative of the both populations.

Both species show relatively high maternity rates when compared to other studies. Mackie et al. (1998:94) reported values ranging from 1.25 to 1.90 fawns per doe for mule deer and 1.50 to 2.0 for white-tailed deer. All females of reproductive age examined in this study were pregnant. Given the relatively high maternity rates observed, neither species seems to be limited by habitat.

Further evidence that neither species is nutritionally stressed is provided by the low occurrence of mortalities attributed to malnutrition. Only 2 of 21 mule deer mortalities were the result of poor animal condition. Only 1 of 13 white-tailed deer mortalities was classified as natural, yet it was ultimately caused by an accident and not malnutrition or poor condition. Mule deer survival was lowest in winter, but cougar

predation and not malnutrition was the highest risk to mule deer during that season (Figure 5). It is possible that mule deer are weakened during winter and therefore more susceptible to cougar predation, however no animals classified as cougar mortalities displayed poor condition as evidenced by poor marrow consistency. Combined, these factors (relatively high maternity and low mortality attributable to poor condition) suggest that this mule deer population's decline was not caused by limited food or habitat.

Predation hypothesis

Adult survival is the most important variable in the growth of any deer population (White and Bartmann 1997; sensitivity analysis this study – see Results: population growth). In several mule deer populations, predation has been found to be the major source of adult mortality (e.g. Bleich and Taylor 1998). Cougar predation was the primary cause of adult mortality in both species in our study area, accounting for 19 of 28 (68%) deaths for which a cause could be determined. As such, predation had the most direct effect on the population growth of both species. Predation rates were significantly higher for mule deer (0.17) than for white-tailed deer (0.09) ($P = 0.06$), suggesting that predation was the cause of this mule deer population's decline.

Density dependent and density independent predation

If predation was density dependent for both mule deer and white-tailed deer, population growth of both species should parallel one another with growth slowing as populations increase because of increased predation pressure. In the last two years of our

study, population growth rates deviated dramatically, with decreases in mule deer growth mirrored by increases in white-tailed deer (Figure 6). The predation rate on mule deer remained high throughout the study regardless of mule deer density (Figure 7) but increased on white-tailed deer as the whitetail population rebounded from the severe winter of 1996/97 (Figure 7). Thus predation appears to be density independent or inversely density dependent on mule deer, and density dependent on white-tailed deer.

Messier (1994) suggested that in multi-prey systems, the functional and numerical response of predators are density-independent of any one prey species, and therefore capable of decreasing prey densities to low equilibrium points. In our study area, the total number of predators is likely set by the total prey population. However, the total predation rate on mule deer seems more strongly tied to the abundance of white-tailed deer than to mule deer. A difference in predation such as this, is consistent with the apparent competition (alternate prey) hypothesis first described by Holt (1977).

Apparent competition

Apparent competition can occur at three spatial/temporal scales (Holt 1994). Predators may be supported by a single prey, but during periods of low availability switch to a secondary prey species. Hamlin et al. (1984) found that coyote predation on mule deer fawns was lowest when rodent populations were high, and Sweitzer et al. (1997) reported near-extinction of porcupines (*Erethizon dorsatum*) from cougar predation following the collapse of a mule deer population following drought. Secondly, predators may move between habitats and encounter different prey. Seip (1992) found that wolves in southeastern B.C. were sustained primarily by moose, but became a major

predator of mountain caribou (*Rangifer tarandus caribou*) during summer when caribou, wolves, and moose occupied similar habitats. Thirdly, invading prey may artificially inflate predator numbers. Holt (1994) showed that if invading animals become the primary prey, the resultant increase in predators may threaten resident alternative prey. This has been modelled (Pech et al. 1995, Namba et al. 1999) and was demonstrated by Sinclair et al (1998:569) in Australia, where an invading rat (*Rattus villosissimus*) caused an increase in foxes (*Vulpes vulpes*), resulting in a “precipitous decline” of other native fauna.

White-tailed deer populations are thought to be increasing across the West (Crete and Daigle 1999), possibly in response to anthropogenic habitat modifications (Roseberry and Woolf 1998). This increase may have placed mule deer in the position of secondary prey described by Holt (1994). As such, mule deer are at risk of disproportionate or compensatory predation, especially following perturbations in white-tailed deer densities (Sweitzer et al. 1997).

Using harvest and hunter effort records for both species we compared population trends over the past 13 years (Figure 8). The population trends of mule and white-tailed deer are positively correlated ($R = 0.62$, $R^2 = 0.38$, $P = 0.02$), however only the white-tailed deer population shows a significant correlation between population trend and winter snow accumulation ($R = 0.58$, $R^2 = 0.34$, $P = 0.04$), the mule deer do not ($R = 0.34$, $R^2 = 0.12$, $P = 0.26$). Further, the same pattern in population growth following the heavy snowfall of 1997 documented during this study, seemed to be repeated in 1993 and 1989. Although 1989 was not a heavy snow year (Figure 8), white-tailed deer numbers may be more strongly driven by environmental stochastic events than mule deer.

Following each decline, the mule deer population failed to recover as quickly as the white-tailed deer (Figure 8). That variations in the white-tailed deer population can be explained by snow accumulations, and trends in mule deer populations cannot, suggests that mule deer are subjected to different population constraints, namely density independent or inversely density dependent predation due to apparent competition.

Traditional theory has stated that cougars are territorial predators that show a strong ability to self regulate their population (Seidensticker et al 1973; Lindzey et al, 1994). Recent research, however, has suggested that this may not hold and that cougars more strongly resemble a migratory generalist that responds to prey/deer densities (Pierce et al. 2000). A time lag in the numerical response of predators can have a dramatic effect on prey population cycling and stability. In general, the greater the time lag (the slower the numerical response) the greater the instability, and the deeper and more chaotic the cycles (Murdoch and Oaten 1975). Mobile predators, with short generation times, will respond most quickly to fluctuations in prey densities and therefore have the quickest numerical responses (Korpimaki and Norrdahl, 1991). As generalist predators, cougars may show a short to intermediate time lag while adjusting their numbers to that of their primary prey. This intermediate time lag may be slow enough to cause disproportionate predation on secondary prey (mule deer) but quick enough to allow primary prey (whitetails) to quickly rebound to a high equilibrium.

The harvest data seems to support the apparent competition hypothesis (Figure 8). On three occasions over the past 12 years, mule deer and white-tailed deer populations have experienced vastly divergent trends in abundance following major perturbations (1988/89, 1992/93, 1996/97). We suggest that the number of cougars in the system is set

by the number of primary prey (white-tailed deer). Following perturbation, mule deer (secondary prey) come under compensatory predation pressure, causing a further decline in the mule deer population until cougar densities adjust to the new white-tailed deer density. As predation is density dependent on white-tailed deer, their numbers quickly rebound under reduced predation pressure.

Management implications

When deer populations are at their lowest, managers often turn their attention to the effects of predators (Carpenter 1997). Despite high hunting pressure on cougars in our study area, (52 cougars were removed from the study area through legal harvest from 1996 to 1999, British Columbia Ministry of Environment Lands and Parks, Cranbrook B.C., unpublished data) predation mortality of mule deer remained seemingly constant (13 to 19%) (Table 2). Although cougars are the proximate cause of mule deer decline, the ultimate cause may be the presence of an abundant, invading, primary prey (white-tailed deer). As long as prey numbers are sufficient, immigration of cougars and other generalist predators may quickly replace harvested animals, thus maintaining high predation pressure on mule deer. Increased cougar harvest may be appropriate following harsh winters to assuage predation pressure on secondary prey (mule deer). Actively adjusting the cougar population to a lower equilibrium may eliminate the lag time in the numerical response of cougars, thus lessening the period of time that mule deer would be under increased predation pressure. However, gradual reductions of white-tailed deer (to prevent prey switching) may provide a more long-term solution to declining mule deer

populations within our study area, and across the west, by directly reducing numbers of generalist predators and indirectly reducing predation pressure on mule deer.

The results and recommendations presented in this paper are not unequivocal because of the small sample sizes, short time series, and lack of experimental replication. We urge other researchers to test for apparent competition in systems where mule deer and white-tailed deer are sympatric, and mule deer are thought to be declining.

Acknowledgements

Funding was provided by the Columbia Basin Fish and Wildlife Compensation Program and Washington State University. We wish to thank E.O. Garton, P.I. Ross, and L. Shipley for valuable comments on the manuscript.

References

- Akcakaya, H.R., Burgman, M.A., and Ginzburg, L.R. 1999. Applied Population Ecology: principles and computer exercises using RAMAS[®] Ecolab. Sinauer Associates, Inc. Sunderland Massachusetts.
- Armleder, H.M., Waterhouse, M.J., Keisker, D.G., and Dawson, R.J. 1994. Winter habitat use by mule deer in the central interior of British Columbia. *Can. J. Zool.* **72**:1721-1725.
- Anthony, R.G. and Smith, N.S. 1977. Ecological relationships between mule deer and white-tailed deer in Southeastern Arizona. *Ecol. Monogr.* **47**:255-277.
- Ballard, W.B., Whitlaw, H.A., Wakeling, B.F., Brown, R.L., deVos, J.C., and Wallace, M.C. 2000. Survival of female elk in northern Arizona. *J. Wildl. Manage.* **64**:500-504.
- Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H., and deVos Jr., J.C. 2001. Deer-predator relationships: a review of recent North American studies with emphasis on mule and black-tailed deer. *Wildl. Soc. Bull.* **29**:91-98.
- Bergerud, A.T., and Elliot, J.P. 1986. Dynamics of caribou and wolves in northern British Columbia. *Can. J. Zool.* **64**:1515-1529.
- Bleich, V.C., and Taylor, T.J. 1998. Survivorship and cause-specific mortality in five populations of mule deer. *Great Basin Naturalist* **58**:265-272.
- Bowden, D.C., Anderson, A.E., and Medin, D.E. 1984. Sampling plans for mule deer sex and age ratios. *J. Wildl. Manage.* **48**:500-509.

- Carpenter, L.H. 1997. Deer in the West. *In* Proceedings of the 1997 deer/elk workshop. Edited by J.C. deVos, Jr. Arizona Game and Fish Department. Phoenix, AZ. pp. 1-10.
- Caughley, G., and Sinclair, A.R.E. 1994. Wildlife ecology and management. Blackwell Science, Inc, Cambridge, Massachusetts, USA.
- Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. N.Y. State Conservation **3**:19-22.
- Clements, C.D., and Young, J.A. 1997. A viewpoint: rangeland health and mule deer habitat. J. Range Manage. **50**:129-138.
- Connolly, G.F. 1981. Assessing populations. *In* Mule and black -tailed deer of North America. Edited by O.C. Wallmo. University of Nebraska Press. Lincoln, NB. pp. 287-345.
- Coupe, R., Stewart, A.C., and Wikeem, B.M. 1991. Englemann spruce – subalpine fir zone. *In* Ecosystems of British Columbia. Edited by D. Meidinger and J. Pojar. Special Report Series 6, B.C. Ministry of Forests, Research Branch, Victoria, B.C. pp. 223-236
- Crete, M., and Daigle, C. 1999. Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production. Acta Vet. Hungarica. **47**:1-16.
- Eberhardt, L.L., and Thomas, J.M. 1991. Designing environmental field studies. Ecol. Monogr. **6**:53-73.

- Garrott, R.A., White, G.C., Bartmann, R.M., Carpenter, L.H., and Alldredge, A.W. 1987. Movements of female mule deer in northwest Colorado. *J. Wildl. Manage.* **51**:634-643.
- Gill, R.B. 1999. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife, Denver, Colorado.
- Hamlin, K.L., Riley, S.J., Pyrah, D., Dood, A.R., and Mackie, R.J. 1984. Relationships among mule deer fawn mortality, coyotes, and alternate prey species during summer. *J. Wildl. Manage.* **48**:489-499.
- Hatter, I.W. and Janz, D.W. 1994. Apparent demographic changes in black-tailed deer associated with wolf-control on northern Vancouver Island. *Can. J. Zool.* **72**:878-884.
- Heaven, P.C., Tinker, M.T., and Adams, I. 1998. Columbia basin fish and wildlife compensation program: ungulate monitoring plan. Columbia Basin Fish and Wildlife Compensation Program, Athlmer, B.C., Canada.
- Heisey, D.M., and Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.* **49**:668-674.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.* **12**:197-229.
- Holt, R.D., and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Ann. Rev. Ecol. Sys.* **25**:495-520.

- Ketcheson, M.V., Braumandle, T.F., Meidinger, D., Utzig, G., Demarchi, D.A, and Wikeem, B.M. 1991. Interior cedar – hemlock zone. *In* Ecosystems of British Columbia. *Edited by* D. Meidinger and J. Pojar. Special Report Series 6, B.C. Ministry of Forests, Research Branch, Victoria, B.C. Pages 167-181
- Kilpatrick, H.J., Spohr, S.M., and DeNicola, A.J. 1997. Darting urban deer: techniques and technology. *Wildl. Soc. Bull.* **25**:542-546.
- Korpimaki, E., and Norrdahl, K. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecol.* **72**:814-826.
- Kunkel, K.E., and Mech, L.D. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. *Can. J. Zool.* **72**:1557-1565.
- Leslie, P.H. 1945. On the use of matrices in certain population mathematics. *Biometrika* **33**:183-212.
- Lindzey, F.G., Van sickle, W.D., Ackerman, B.B., Hemker, T.P., and Laing, S.P. 1994. Cougar population dynamics in southern Utah. *J. Wildl. Manage.* **58**:619-624.
- Loison, A., and Langvatn, R. 1998. Short and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* **116**:489-500.
- Mackie, R.J., Pac, D.F., Hamlin, K.L., and Dusek, G.L. 1998. Ecology and management of mule deer and white-tailed deer in Montana. *Montana Fish, Wildlife and Parks*. Federal Aid Project W-120-R. Helena, Montana.
- McCorquodale, S.M. 1999. Movements, survival, and mortality of Black-tailed deer in the Klickitat Basin of Washington. *J. Wildl. Manage.* **63**:861-871.

- McCullough, D.R., Pine, D.S., Whitmore, D.L., Mansfield, T.M., and Decker, R.H. 1990. Linked sex harvest strategy for big game management with a test case on black-tailed deer. *Wildl. Monogr. No. 112.*
- McCullough, D.R. 1992. Concepts of large herbivore population dynamics. *In Wildlife 2001: Populations. Edited by D.R. McCullough and R.H. Barrett. Elsevier Science Publishers, Ltd., London, England. pp. 967-984*
- McNay, R.S., and Voller, J.M. 1995. Mortality causes and survival estimates for adult female columbian black-tailed deer. *J. Wildl. Manage.* **59**:138-146.
- Meidinger D., and Pojar, J. 1991. *Ecosystems of British Columbia. Special Report Series 6, B.C. Ministry of Forests, Research Branch, Victoria, B.C.*
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecol.* **75**:478-488.
- Murdoch, W.W. and Oaten, A. 1975. Predation and stability. *Advances in Ecological Research.* **9**:1-131.
- Namba, T., Umento, A., and Minami, E. 1999. The effects of habitat fragmentation on persistence of source-sink metapopulations in systems with predators and prey or apparent competitors. *Theor. Pop. Biol.* **56**:123-137.
- Nelson, M.E. and Mech, L.D. 1986. Mortality of white-tailed deer in northeastern Minnesota. *J. Wildl. Manage.* **50**:691-698.
- O’Gara, B.W. 1978. Differential characteristics of predator kills. *In Proceedings of the eighth biennial pronghorn antelope workshop, Jasper, Alberta, May 2-4, 1978. Alberta Department of Recreation, Parks and Wildlife, Edmonton. pp. 380-393*

- Pauley, G.R., Peek, J.M., and Zager, P. 1993. Predicting white-tailed deer habitat use in northern Idaho. *J. Wildl. Manage.* **57**:904-913.
- Pech, R.P., Sinclair, A.R.E., and Newsome, A.E. 1995. Predation models for primary and secondary prey species. *Wildl. Res.* **22**:55-64.
- Pierce, B.M., Bleich, V.C., and Bowyer, R.T. 2000. Social organization of mountain lions: does a land-tenure system regulate population size. *Ecol.* **81**:1533-1543.
- Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. *J. Wildl. Manage.* **53**:7-15.
- Roseberry, J.L., and Woolf, A. 1998. Habitat-population density relationships for white-tailed deer in Illinois. *Wildl. Soc. Bull.* **26**:252-258.
- Roffe, T.J., Friend, M., and Locke, L.N. 1996. Evaluation of causes of wildlife mortality. *In* Research and management techniques for wildlife and habitats. *Edited by* T.A. Bookhout. Fifth ed., rev. The Wildlife Society, Bethesda, Md. pp. 324-348
- Sauer, J.R., and Williams, B.K. 1989. General procedures for testing hypotheses about survival or recovery rates. *J. Wildl. Manage.* **53**:137-142.
- Samuel, M.D., Garton, E.O., Schlegal, M.W., and Carson, R.G. 1987. Visibility bias during aerial surveys of elk in northcentral Idaho. *J. Wildl. Manage.* **51**:622-630.
- Samuel, M.D., Steinhorst, R.K., Garton, E.O., and Unsworth, J.W. 1992. Estimation of wildlife population ratios incorporating survey design and visibility bias. *J. Wildl. Manage.* **56**:718-725.

- Schmidt, K.A. and Whelan, C.J. 1998. Predator-mediated interactions between and within guilds of nesting songbirds: experimental and observational evidence. *Am. Nat.* **152**:395-402.
- Seidensticker, J.C., Hornocker, M.G., Wiles, H.V., and Messick, J.P. 1973. Mountain lion social organization in the Idaho Primitive Area. *Wildl. Monogr.* No. 35.
- Seip, D.R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. *Can. J. Zool.* **70**:1494-1503.
- Short, H.L. 1981. Nutrition and Metabolism. *In* Mule and black-tailed deer of North America. *Edited by* O.C. Wallmo. University of Nebraska Press. Lincoln. pp. 99-127
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P., and Newsome, A.E. 1998. Predicting effects of predation on conservation of endangered prey. *Cons. Biol.* **12**: 564-575.
- Sinclair, A.R.E., and Pech, R.P. 1996. Density dependence, stochasticity, compensation and predator regulation. *Oikos* **75**:164-173
- Solomon, M.E. 1949. The natural control of animal populations. *The Journal of Animal Ecol.* **18**:1-35.
- Swenson, J.E., Knapp, S.J., and Wentland, H.J. 1983. Winter distribution and habitat use by mule deer and white-tailed deer in Southeastern Montana. *Prairie Nat.* **15**:97-112.

- Sweitzer, R.A., Jenkins, S.H., and Berger, J. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in the Great Basin Desert. *Cons. Biol.* **11**:1407-1417.
- Unsworth, J.W., Leban, F.L., Leptich, D.J., Garton, E., and Zager, P. 1994. Aerial survey: user's manual with practical tips for designing and conducting aerial big game surveys, second edition. Idaho Department of Fish and Game, Boise, Idaho.
- Unsworth, J.W., Pac, D.F., White, G.C., and Bartmann, R.M. 1999. Mule deer survival in Colorado, Idaho, and Montana. *J. Wildl. Manage.* **63**:315-326.
- White, G.C., and Bartmann, R.M. 1997. Mule deer management – what should be monitored? *In Proceedings of the 1997 Deer/Elk Workshop. Edited by James C. deVos, Jr.* Arizona Game and Fish Department. Phoenix. pp. 104-118
- Wood, A.K., Mackie, R.J., and Hamlin, K.L. 1989. Ecology of sympatric populations of mule deer and white-tailed deer in a prairie environment. Montana Department of Fish, Wildlife & Parks. 98pp.
- Woods, G.P., 1984. Habitat selection of white-tailed deer in the Pend d'Oreille Valley, British Columbia. Thesis, University of Idaho, Moscow, Idaho, USA.
- Zar, J.H. 1984. *Biostatistical Analysis*. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.
- Zeigler, D.L. 1978. The Okanogan mule deer. Washington Department of Game. Biological Bulletin No. 15. 106 pp.
- Zender, S. 1987. Summary of data collected on Stevens County road-killed white-tailed deer. Washington Fish and Game, Spokane Regional Office.

Table 1. Number and sex of deer radiocollared, and radiodays accumulated in each year of the study in south-central British Columbia, 1997-2000.

Year	White-tailed Deer			Mule Deer		
	Female	Male	Radiodays	Female	Male	Radiodays
1997	18	0	6,153	18	1	4,603
1998	23	1	6,191	19	3	4,741
1999	22	2	6,839	21	9	6,663
2000	15	1	3,938	18	6	7,691
Total	25	2	23,121	33	10	23,698

Table 2. Number of mortalities (associated cause specific annual mortality rate), and annual survival rates of mule deer in south-central British Columbia, 1997-2000.

Year	Cause					Total Mortalities	Survival Rate
	Cougar	Other Predation	Natural	Vehicle	Unknown		
1997	2 (0.13)	0	1 (0.06)	0	3 (0.19)	6	0.62
1998	2 (0.13)	2 (0.13)	0	1 (0.06)	0	5	0.68
1999	4 (0.19)	0	1 (0.05)	0	1 (0.05)	6	0.72
2000	3 (0.13)	0	0	1 (0.04)	0	4	0.83
Total	11(0.14)	2 (0.03)	2 (0.03)	2 (0.03)	4 (0.05)	21	0.72

Table 3. Number of mortalities, associated cause specific mortality rates, and annual survival of white-tailed deer in south-central British Columbia, 1997-2000.

Year	Cause					Total Mortalities	Survival Rate
	Cougar	Other Predation	Natural	Vehicle	Unknown		
1997	1 (0.06)	0	0	0	1 (0.06)	2	0.88
1998	1 (0.06)	0	0	0	0	1	0.94
1999	2 (0.09)	0	0	2 (0.09)	1 (0.05)	5	0.77
2000	2 (0.15)	0	1 (0.07)	2 (0.15)	0	5	0.63
Total	6 (0.09)	0	1 (0.01)	4 (0.06)	2 (0.03)	13	0.81

Table 4. Cause specific mortality rates (variance) for mule deer and white-tailed deer in south-central British Columbia, 1997-2000, one tailed binomial z score and associated probabilities (unknown mortalities were censored from the data).

Mortality Cause	Mule Deer Mortality (variance)	White-tailed Mortality (variance)	Z score	P value
Cougar	0.15 (0.00178)	0.09 (0.00118)	1.18	0.12
Other Predation	0.03 (0.00037)	0.00 (0.00000)	1.42	0.08
Natural	0.03 (0.00037)	0.01 (0.00021)	0.54	0.30
Vehicle	0.03 (0.00037)	0.06 (0.00081)	0.90	0.18
Survival	0.76 (0.00249)	0.84 (0.00198)	1.11	0.13

Table 5. Cause specific mortality rates (variance) for mule deer and white-tailed deer in south-central British Columbia from 1997 to 2000, one tailed binomial z score and associated probabilities, using only two mortality classes, predation and others (unknowns are grouped with others).

Mortality Cause	Mule Deer Mortality (variance)	White-tailed Mortality (variance)	Z score	P value
Predation	0.17 (0.00186)	0.09 (0.00111)	1.57	0.06
Other	0.11 (0.00124)	0.10 (0.00128)	0.11	0.46
Survival	0.72 (0.00261)	0.81 (0.00215)	1.32	0.09

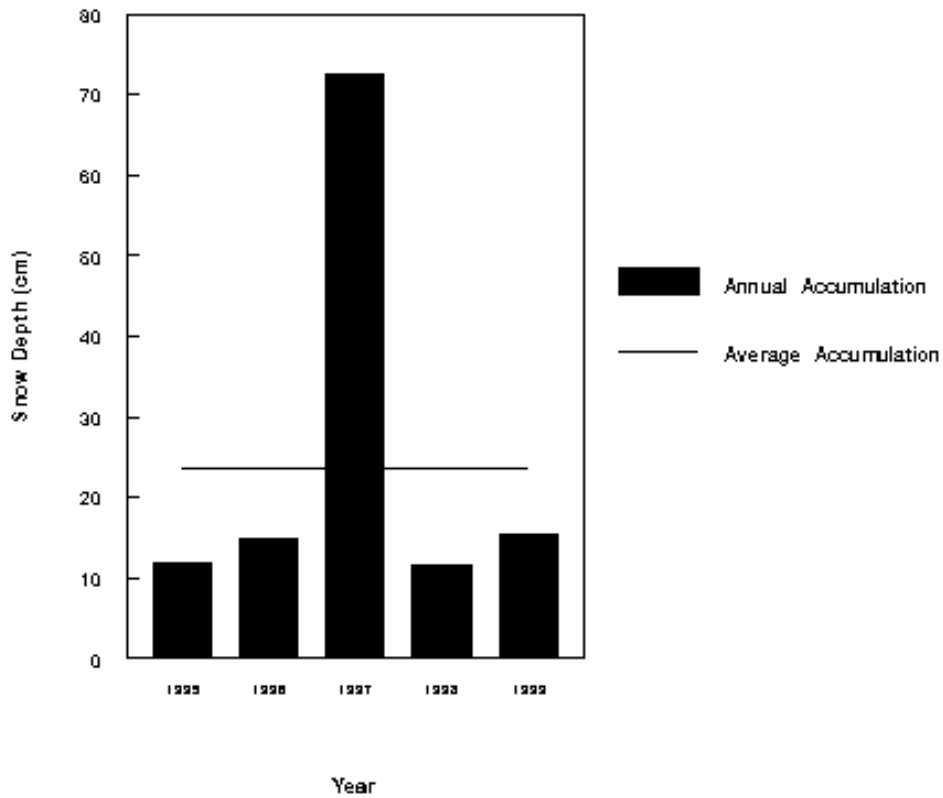


Figure 1. Average (30 yrs) and annual accumulated snow (at months end January to April) recorded at two weather stations (Creston and Castlegar A) in south-central British Columbia 1995 to 1999 (Environment Canada, Vancouver B.C.).

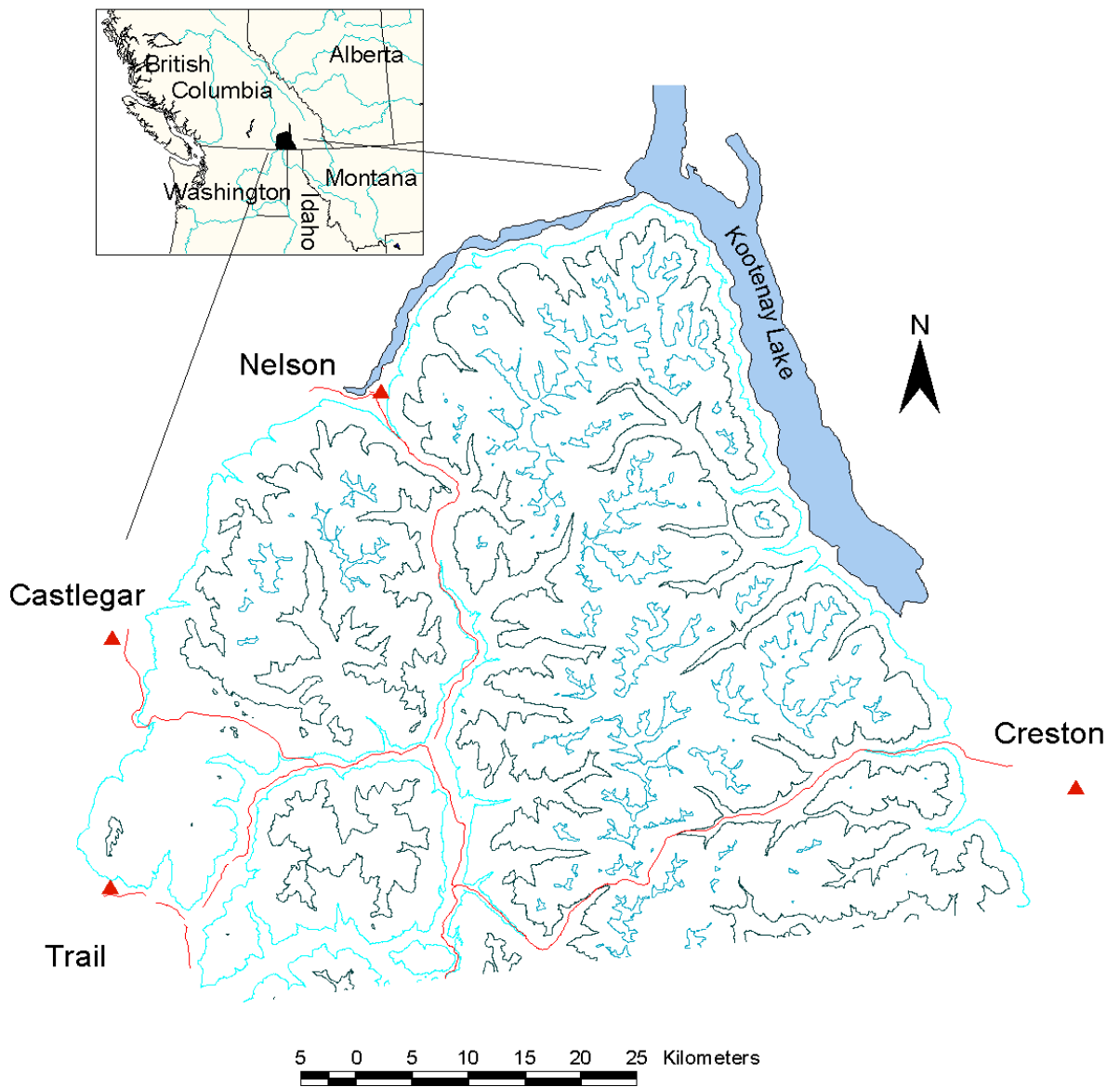


Figure 2. Location and relief (contours = 600 m) of study area in south-central British Columbia, Canada.

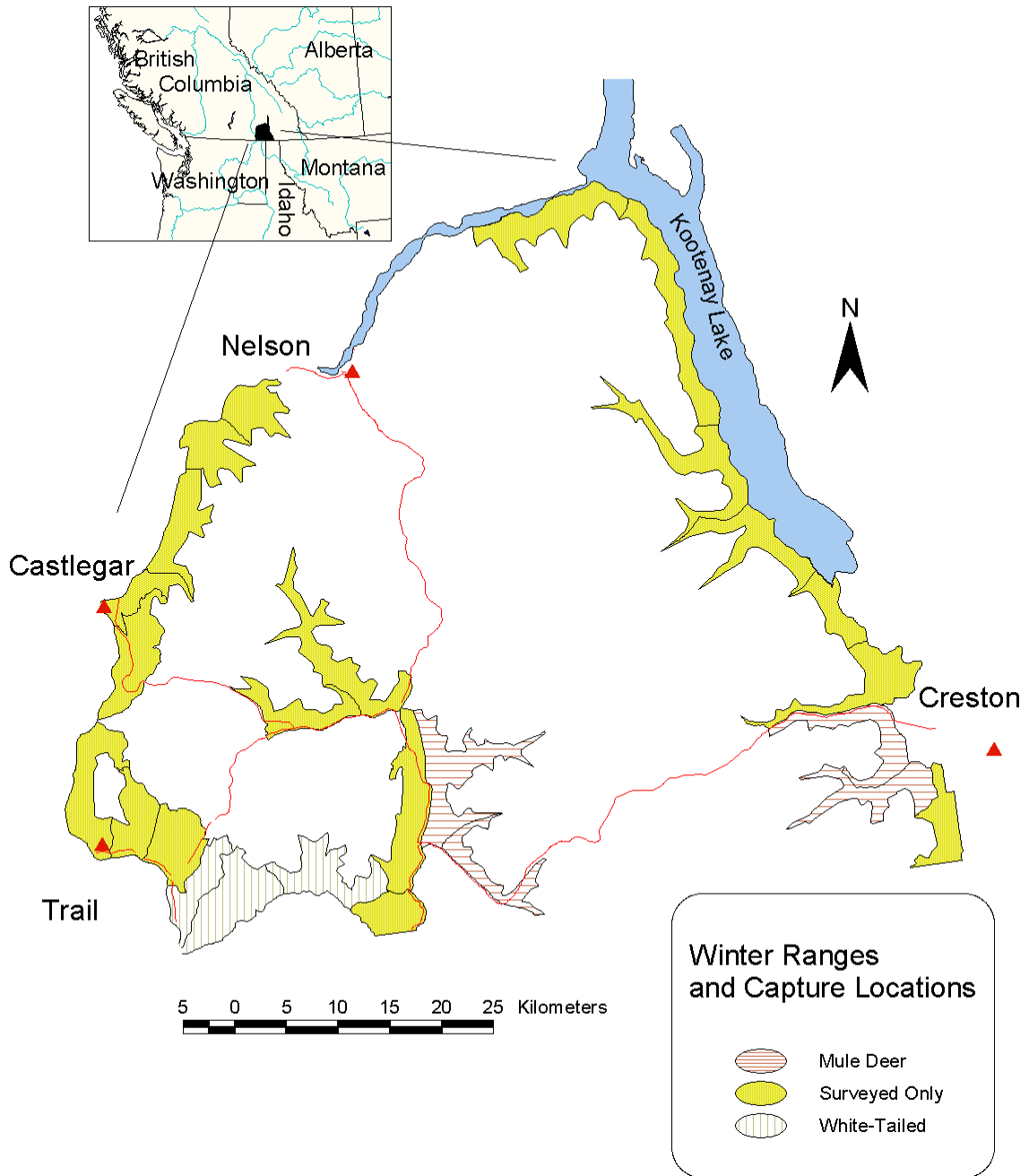


Figure 3. Deer winter ranges, where trapping efforts were concentrated for mule deer and white-tailed deer (February – March 1997-2000), and flown during aerial survey (February, 2000).

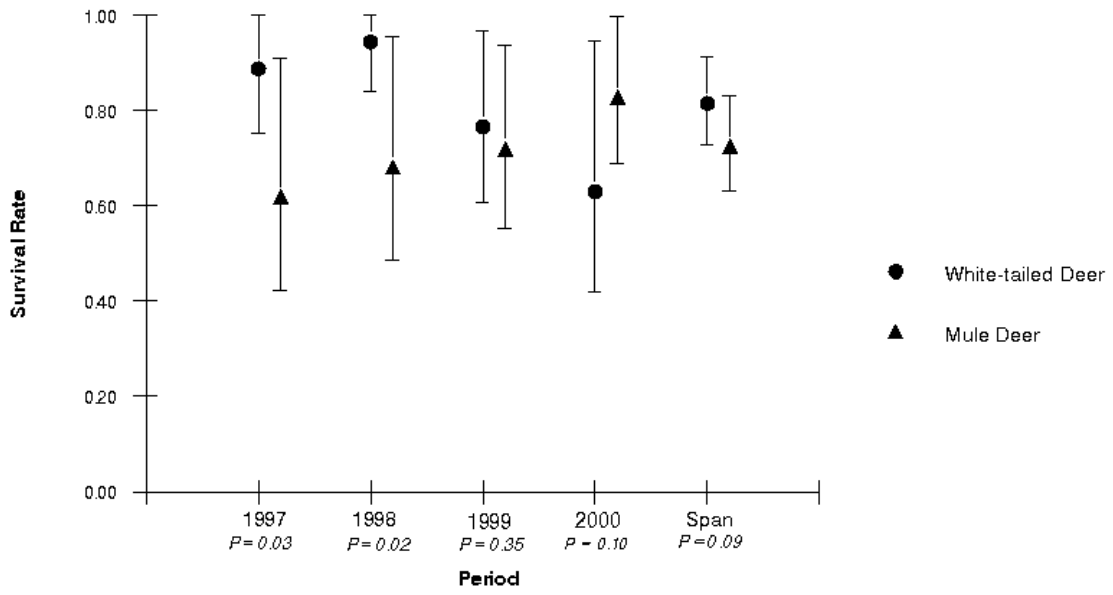


Figure 4. Annual and mean annual (span rate) survival rates, 95% confidence intervals and probabilities of one tailed binomial z tests for mule and white-tailed deer in south-central British Columbia, 1997-2000.

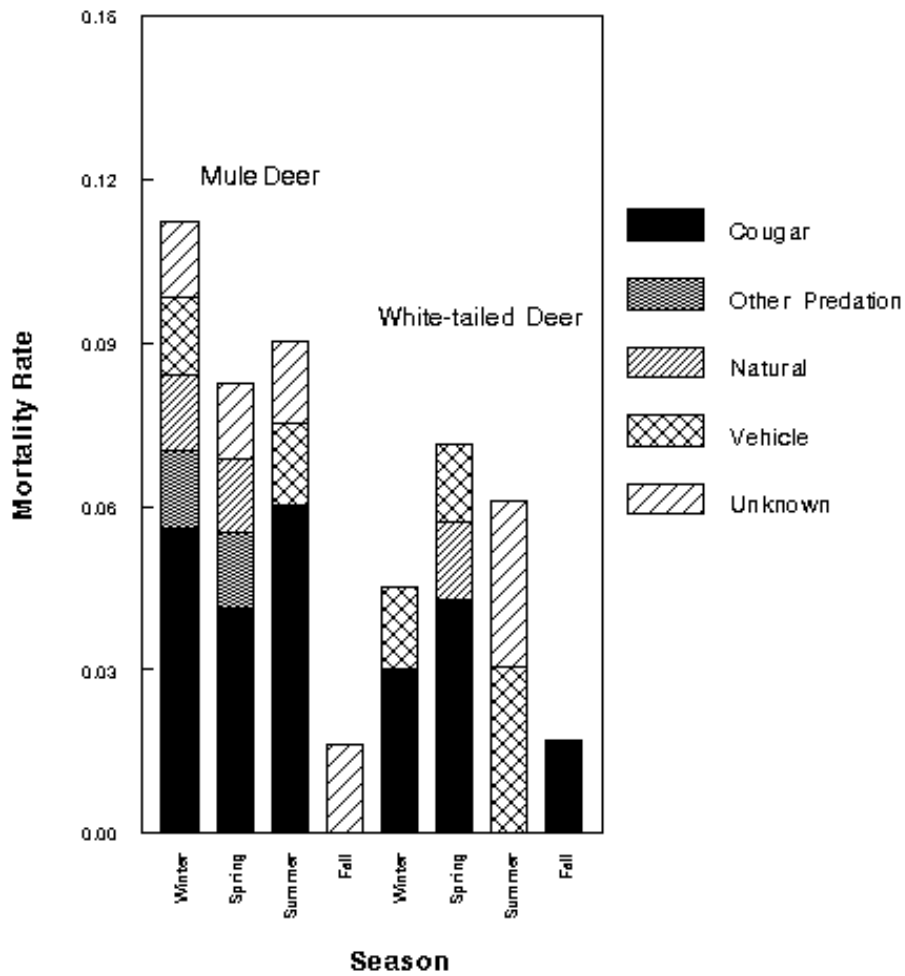


Figure 5. Seasonal cause-specific mortality rates for mule and white-tailed deer in south-central British Columbia, 1997-2000 (survival = 1 – total mortality).

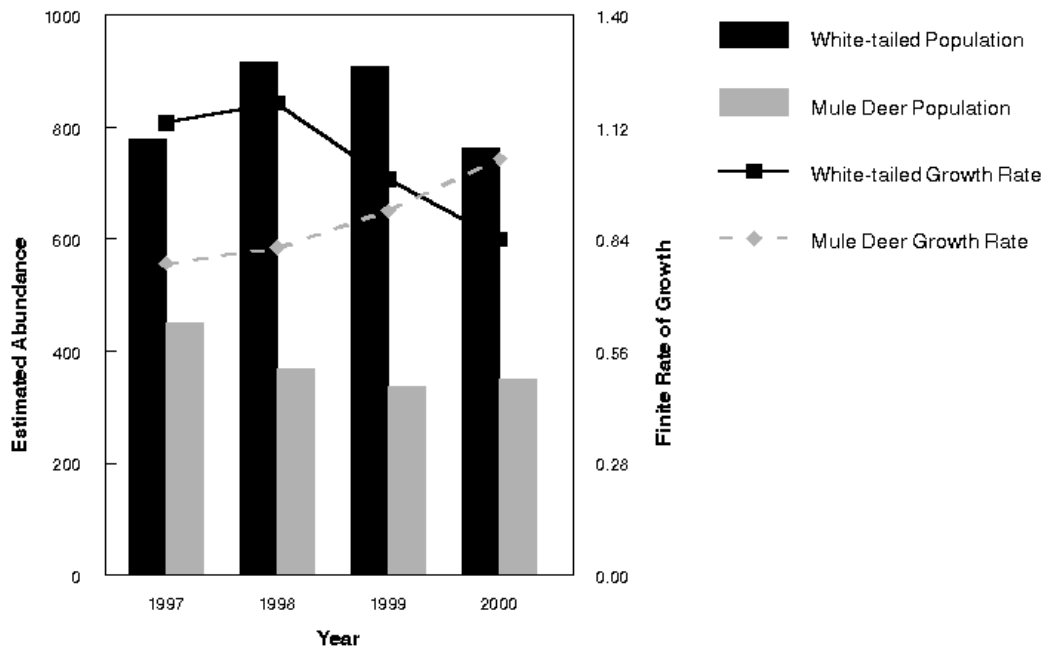


Figure 6. Annual growth rates and relative abundance of mule deer and white-tailed deer in south-central British Columbia, calculated using annual mortality rates, and fecundity and base population rates estimated from aerial survey, February 2000.

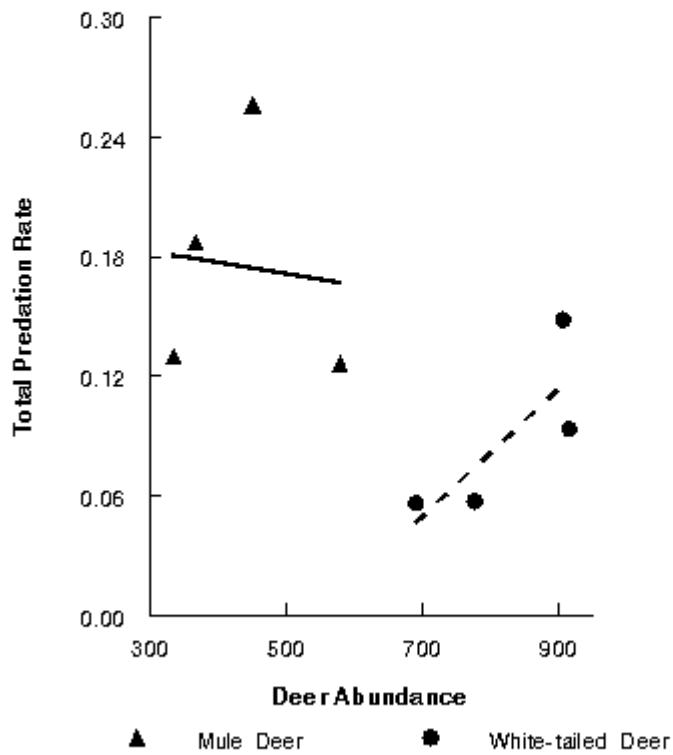


Figure 7. Total predation rates and associated linear trend lines, plotted against density of mule deer (solid line) and white-tailed deer (broken line) in south-central British Columbia, 1997-2000.

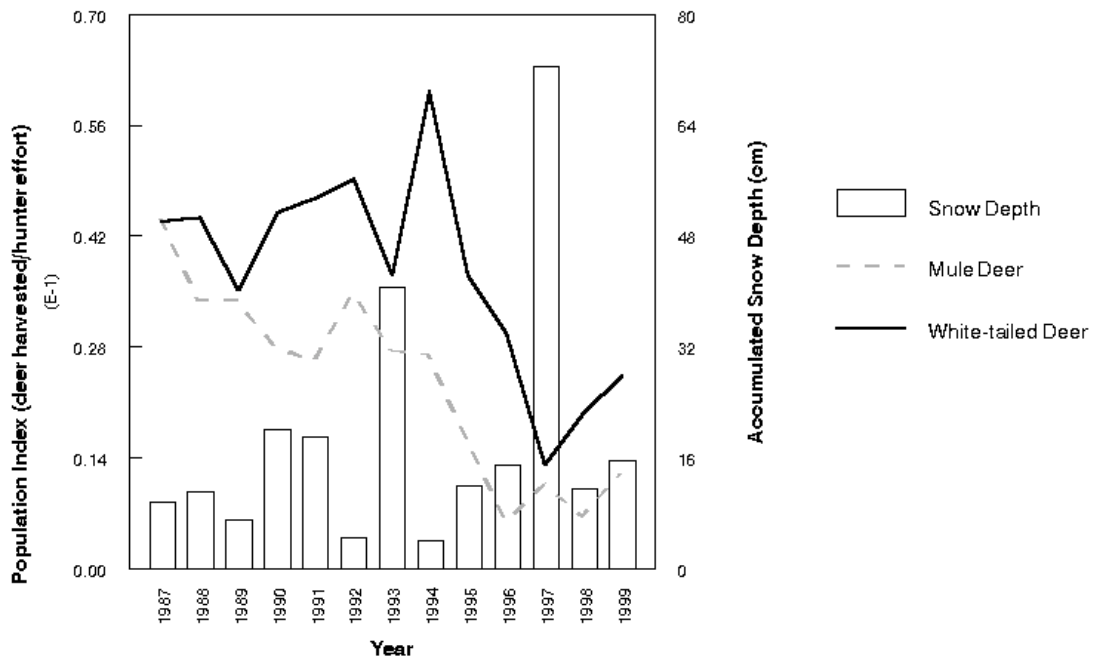


Figure 8. Population index of mule and white-tailed deer (Ministry of Environment Lands and Parks, Cranbrook, British Columbia, Canada, unpublished data) in relation to snow accumulation (January to April) 1987 to 1999 (species specific deer tags were not sold prior to 1987).