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

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

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

Abstract: Mule deer (*Odocoileus hemionus*) populations throughout the west appear to be declining, whereas white-tailed deer (*Odocoileus virginianus*) populations are increasing. We compared abundance, number of fetuses per female (maternity rate), recruitment, and cause-specific adult (≥1 year old) mortality rate for sympatric mule deer and white-tailed deer in south-central British Columbia to assess population growth for each species. White-tailed deer were three times more abundant (908 ± 152) than mule deer (336 ± 122) (mean ± 1 SE). Fetal rates of white-tailed deer (1.83) were similar to those of mule deer (1.78). There was no statistically significant difference in recruitment of white-tailed deer (56 fawns : 100 does) and mule deer (38 fawns : 100 does). The annual survival rate for adult white-tailed deer ($S_{WT} = 0.81$) was significantly higher than that for mule deer ($S_{MD} = 0.72$). The main cause of mortality in both populations was cougar predation. The lower mule deer survival rate could be directly linked to a higher predation rate (0.17) than for white-tailed deer (0.09). The finite growth rate (λ) was 0.88 for mule deer and 1.02 for white-tailed deer. The disparate survival and predation rates are consistent with the apparent-competition hypothesis.

Résumé : Les populations de cerfs mulets (*Odocoileus hemionus*) semblent être en déclin dans tout l'ouest, alors que celles des cerfs de Virginie (*Odocoileus virginianus*) augmentent. Nous avons comparé l'abondance, le taux de production de fétus, le taux de recrutement et les taux de mortalité des adultes (≥1 an) attribuables à des causes spécifiques chez des cerfs mulets er des cerfs de Virginie vivant en sympatrie dans le centre sud de la Colombie-Britannique afin d'évaluer la croissance démographique de chacune de ces espèces. Les cerfs de Virginie sont trois fois plus abondants (908 ± 152) que les cerfs mulets (336 ± 122) (moyenne ± 1 erreur type). Le taux foetal est semblable chez les cerfs de Virginie (1,83) et les cerfs mulets (1,78). Il n'y a pas de différence statistiquement significative entre les taux de recrutement des cerfs de Virginie (56 faons : 100 femelles) et des cerfs-mulets (38 faons : 100 femelles). La survie annuelle des adultes est significativement plus élevée chez le cerf de Virginie ($S_{WT} = 0,81$) que chez le cerf mulet ($S_{MD} = 0,72$). La principale cause de mortalité chez les deux populations est la prédation exercée par les couguars. Le taux de survie plus faible du cerf mulet peut être relié directement à son taux de prédation plus élevé (0,17) que celui du cerf de Virginie (0,09). Le taux de croissance réel (λ) est de 0,88 chez le cerf mulet et de 1,02 chez le cerf de Virginie. La disparité des taux de prédation et de survie est en accord avec l'hypothèse de la compétition apparente.

[Traduit par la Rédaction]

Introduction

Mule deer (*Odocoileus hemionus*) populations are believed to be decreasing, while white-tailed deer (*Odocoileus virginianus*) are increasing, throughout North America (Gill 1999). In a recent survey, 45% of the jurisdictions polled reported decreasing populations of mule deer (Crête and Daigle 1999). By contrast, only 13% reported decreasing white-tailed deer populations, most (52%) reporting increasing white-tailed deer populations. The reason for the concurrent declines in mule deer populations and increases in white-tailed deer populations remains unclear. Indirect and direct competition for resources between the two species does not

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appear to be significant. For instance, Anthony and Smith (1977) and Swenson et al. (1983) described habitat segregation between the species, even when populations were allopatric. Habitat segregation, therefore, usually prevents direct competition. When direct competition between deer species does occur, mule deer appear to be dominant (Anthony and Smith 1977; Wood et al. 1989).

It has been suggested that the quality and availability of mule deer habitat have 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, the quality of white-tailed deer habitat 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 being capable of causing mule deer declines.

During the winter of 1996–1997, extreme snowfall (Fig. 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 have recovered quickly, whereas the mule deer population appeared to continue to
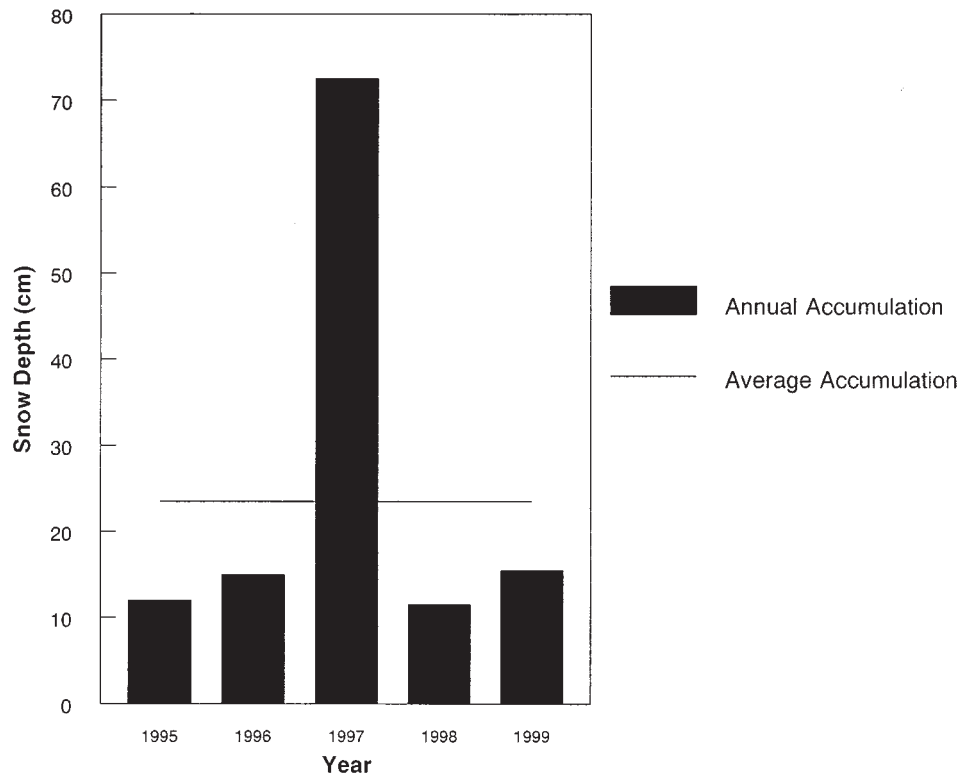
Fig. 1. Average (30 year) and annual accumulated snowfall (at month's end, January–April) recorded at two weather stations (Creston and Castlegar A) in south-central British Columbia, 1995–1999 (Environment Canada, Vancouver, B.C.).

decline (G. Woods, British Columbia Ministry of Water, Land, and Air Protection, Nelson, personal communication). 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 4 categories: (1) human harvest (Caughley and Sinclair 1994, p. 286); (2) stochastic events that are density-independent (Unsworth et al. 1999); (3) food and habitat limitation, which is density-dependent if habitat quality is stable (McCullough et al. 1990; Mackie et al. 1998); and (4) predation, which can be density-dependent, density-independent, or inversely density-dependent (Messier 1994). Predation is often the leading cause of adult mortality in deer populations (for example, see 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 for both deer species, and if any divergence in growth rates existed, to identify the most likely cause. We tested 4 plausible hypotheses to assess which of the above factors were most limiting for mule deer populations in south-central British Columbia: (1) overhunting; (2) environmental stochastic effects; (3) limited resources 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 overhunting hypothesis predicts that any observed decline in mule deer is due to human-caused mortality. If excessive hunting is causing mule deer populations to decline, most mortalities of adults 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 will be 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 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 the effect of the environment on vital rates (e.g., reproduction, natural mortality). If stochastic events affect mule deer more dramatically than white-tailed deer, the correlation between survival and winter severity should be greater for mule deer than for white-tailed deer.

The limited resources/poor 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 of 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), over-winter survival rates should be lower than for white-tailed deer, with most winter mortality caused by malnutrition (Short 1981). Furthermore, maternity and recruitment levels should also be lower for mule deer because of poor female condition (Connolly 1981, p. 247).

The predation hypothesis predicts that differences in

population growth will be caused by differences in predation rate. If predation is limiting, it should be the primary cause of mortality of adult mule deer. Maternity rates should be high, whereas recruitment should be low. Following the severe population reductions in the winter of 1996–1997, 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 predator functional response (number of kills per predator per unit time) and numerical response (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 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 alternative 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°06′N, 116°31′W) and Castlegar (49°18′N, 117°38′W), just north of the Washington–Idaho border (Fig. 2). It encompassed approximately 4000 km², including the Corn Creek drainage, Pend d'Oreille and South Salmo rivers, and headwaters of the Upper Priest River. The physiography of the area is mountainous, with elevations ranging from 450 to 2165 m.

The climate is Pacific Maritime / Continental, with most annual precipitation falling in the form of snow (Environment Canada, Vancouver, British Columbia). Environment Canada maintains weather stations on the east (Creston) and west (Castlegar) edges of the study area and provided the following data. Mean (1961–1990) 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 (1961–1990) annual snowfall is 140.6 cm in Creston (elevation 597 m) and 224.6 cm in Castlegar (elevation 494 m).

The study area lies within two biogeoclimatic zones: interior cedar – hemlock (ICH) and Engelmann spruce – subalpine fir (ESSF) (Meidinger and Pojar 1991). The ICH zone extends from the lowest elevations of the study area to approximately 1200 m. Western red-cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) are the dominant tree species in mature forests, with black cottonwood (*Populus balsamifera trichocarpa*) the climax in moister 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 1200 to 2100 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 reduced the main source of natural disturbance. The last major fires in the area occurred in the 1930s and the forests have now regenerated

to mixed coniferous stands (Woods 1984). Timber has been harvested in the area since the turn of the 20th century, and forestry is now the dominant form of disturbance.

The combination of climate and physiography creates 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 a 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 (900–1200 m) are almost exclusively occupied by mule deer, whereas lower elevation ranges (≤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 zone during summer, with mule deer at an average maximum elevation of 1800 m in early October. The elevation range of white-tailed deer is not quite as high, but they have been observed up to 1700 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.

Deer harvest was permitted throughout the study area except as dictated by private land owners. Mule deer bucks were hunted from 10 September to 31 October annually. White-tailed deer bucks were hunted from 10 September to 30 November during each year of the study. A limited-entry hunt for white-tailed deer does was conducted in 1997 from 10 October to 10 December and again in 2000 from 1 November to 20 December.

Methods

Trapping and monitoring

The Columbia Basin Fish and Wildlife Compensation Program began radio-collaring and monitoring deer in February 1997. Both mule deer and white-tailed deer were added to the sample each winter in an attempt to achieve a sample size of 40–50 animals of each species (Pollock et al. 1989). Deer were captured on winter ranges (Fig. 2) 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 radio-telemetry 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-h delay (Lotek Inc., Newmarket, Ontario). Through a combination of aerial and ground telemetry, deer were checked for mortality signals daily during spring and summer. The frequency of monitoring was reduced in winter to every 2 or 3 days because of the reduced risk of carcasses being scavenged in the absence of bears. Any deer that died within 7 days of

Fig. 2. Deer winter ranges, where trapping efforts were concentrated for mule deer and white-tailed deer (February–March in 1997–2000) and flown during aerial survey (February 2000).
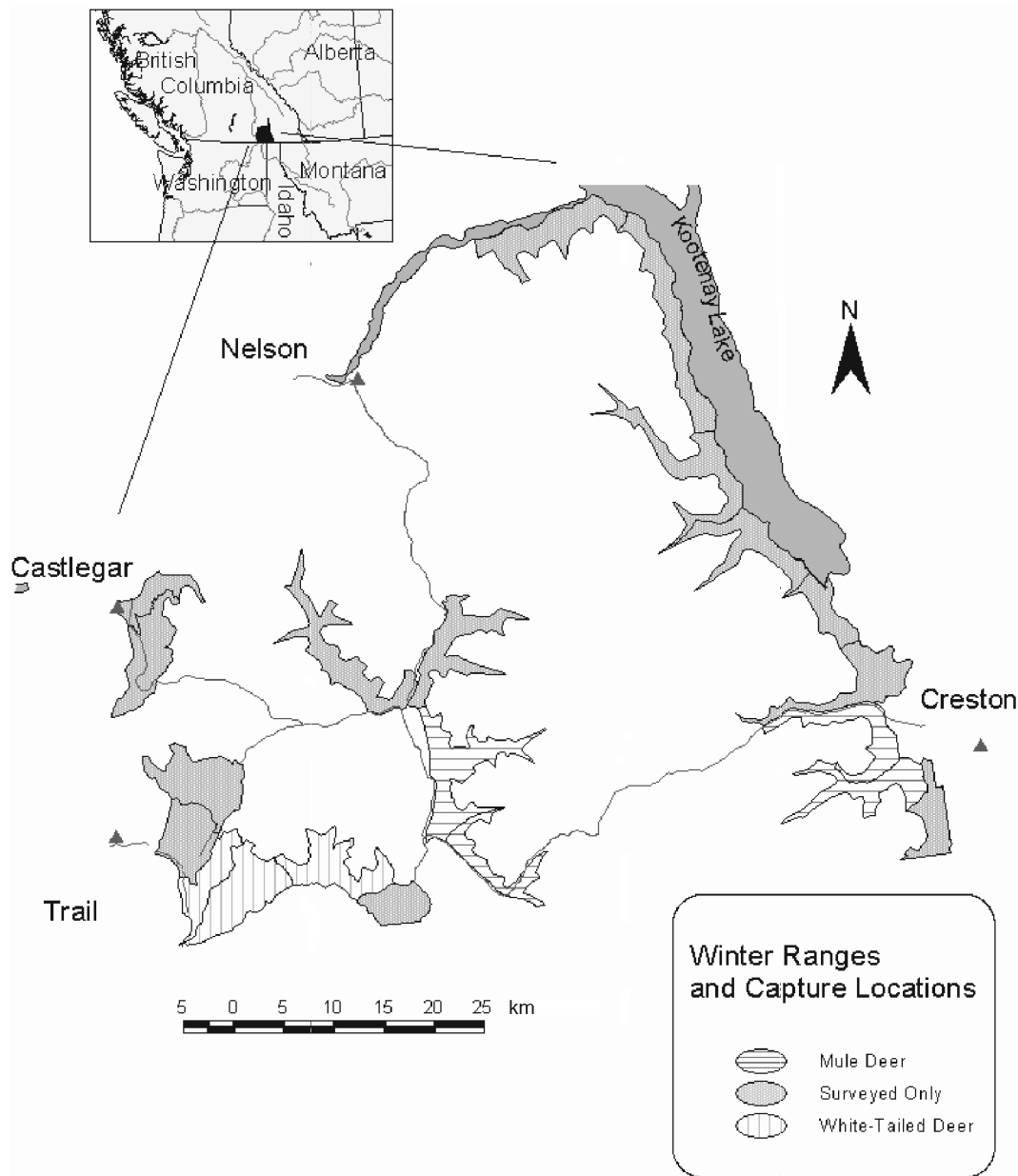
handling was censored from the database. All animals were handled in accordance with Washington State University Animal Care Permit No. 2843.

Adult mortality

Mortality signals were normally investigated within 24 h. Cause of death was established on the basis of 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). Femur marrow consistency was visually assessed as an indication of health at time of death (Cheatum 1949).

The 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 obtain sufficient data to analyse seasonal survival, we pooled seasonal data across all 4 years of the study. Seasons were divided into summer (1 July to 20 September), fall migration/rut (1 October to 31 December), winter (1 January to 30 April), and spring migration (1 May to 30 June) based on the movement patterns of radio-collared mule deer (e.g., Garrott et al. 1987). One-tailed binomial z tests were used to test the null hypothesis that mule deer mortality rates were less than or equal to ($\leq$) those of white-tailed deer (Zar 1984, p. 101; Nelson and Mech 1986). Simple regression was used to test for a correlation between annual survival rates of adults of the two species. A higher human-caused mortality rate for mule deer would support the overhunting hypothesis. A higher natural mortality rate for mule deer would support the

stochastic-event and (or) resource limitation/poor habitat hypothesis. A higher predator-caused mortality rate for mule deer would support the predation hypothesis.

Reproduction and maternity

Radio-collared mortalities and road-killed does were examined for fetuses prior to parturition (1 June) to determine maternity rate. Fawn mortality rates were 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 variance was used to test for differences in maternity rates. Maternity is considered an indication of doe health and therefore of habitat quality. Lower maternity rates in mule deer would suggest that they were disadvantaged because of poor habitat quality, thus supporting the limited resources/poor 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) (Fig. 2). Fawns were considered recruits at 9 months of age (only after they were exposed to mortality factors similar to those affecting adults) (Bergerud and Elliot 1986). Over-winter survival rates for deer are 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 to ensure 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 stratum was surveyed from 12 to 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 the 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 of sex and age ratios as well as relative abundance of both species, we used the mule deer Hiller 12-E Idaho (winter) sightability model contained in the program. Sightability models are designed to account for unseen animals in aerial surveys. An estimate of the number of animals present during the survey but missed by the observer is based on amount of vegetative cover, vegetation class (i.e., shrub, conifer, etc.), snow cover, group size, and activity of the animal (running, standing, or walking) during each observation. Unfortunately we were unable to obtain a sightability model for white-tailed deer in our area, and lacked the resources to develop one of our own. We believe, however, that because of similarities in vegetation, survey timing, and consistency of observers, our survey is equally applicable to the two species of deer. If differences do exist, white-tailed deer may be more secretive and possibly harder

to spot than mule deer, leading to underestimation of their actual numbers relative to those of mule deer.

Difference in recruitment was tested using the χ^2 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 prebreeding model in RAMAS GIS (Akcakaya et al. 1999). In a prebreeding model, the earliest age class in the matrix is almost 1 year old (Akcakaya et al. 1999:138). Fecundity rates were one-half (as this was a female-only model) the total recruitment rate. This assumes that an equal number of male and female fawns were born in the previous spring. Fecundity of 1-year-olds was assumed to be one-half that observed in adults, as this would be their first breeding season (Carpenter 1997; Mackie et al. 1998, p. 95). Because of limitations on age-specific maternity and survival rates, we assumed that all females 2+ years old had the same fecundity and survival rates. Adult female survival rates were calculated using MICROMORT by censoring all males from the dataset. For both white-tailed deer and mule deer, the maximum age was set at 13 years. 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 (Akcakaya et al. 1999, p. 56). Mean geometric (span) and annual growth rates were calculated for each year, based on the above method.

White-tailed deer drop their antlers earlier than mule deer. During an aerial survey this may cause observers to unwittingly classify some white-tailed deer bucks as does. This would lead to overestimation of the actual number of does and corresponding underestimation of the fawn:doe ratio or recruitment rate. As a result our population model may underestimate the white-tailed deer growth rate.

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.

We tested our population-trend estimates by comparing our model with harvest records collected by British Columbia Ministry of Water, Land and Air Protection (Cranbrook). This measure of relative abundance of both species was constructed by dividing the number of animals harvested by the number of hunter-days (effort) accumulated in management units 4-07 and 4-08 from 1987 to 1999.

Density-dependent versus 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 the predation rate will increase with prey density. The density independent, or inversely den-

Table 1. Numbers and sex of radio-collared deer, and radio-days accumulated in each year of the study in south-central British Columbia, 1997–2000.

Year	White-tailed deer			Mule deer		
	No. of females	No. of males	No. of radio-days	No. of females	No. of males	No. of radio-days
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. Numbers of mortalities and annual survival rates for mule deer in south-central British Columbia, 1997–2000.

Year	Cause					Total no. of mortalities	Survival rate
	Cougar predation	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

Note: Values in parentheses show the associated cause-specific annual mortality rate.

Table 3. Numbers of mortalities and annual survival rates for white-tailed deer in south-central British Columbia, 1997–2000.

Year	Cause					Total no. of mortalities	Survival rate
	Cougar predation	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

Note: Values in parentheses show the associated cause-specific annual mortality rate.

sity dependent, predation hypothesis predicts that the predation rate will remain stable or increase with decreasing prey density (Messier 1994).

Results

Trapping success and sample size

From March 1997 to March 2000, 43 mule deer and 27 white-tailed deer were radio-collared and monitored. The total numbers of animals and radio-days for each year of the 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 predation, other predation (including one bobcat and one unknown predator), natural (two mortalities, 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 predation, other predation, natural (one accidental injury to 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. As with mule deer, no radio-collared white-tailed deer were harvested during the study.

The annual survival rate for mule deer ($S_{1997} = 0.62$ and $S_{1998} = 0.68$) was lower than that for white-tailed deer ($S_{1997} = 0.89$ and $S_{1998} = 0.94$) during the first 2 years of the 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 2 years of the study, the white-tailed deer survival rate decreased ($S_{1999} = 0.77$ and $S_{2000} = 0.63$), whereas that for mule deer 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 the mule deer survival rate was actually higher in 2000 ($z_{2000} = 1.30$, df = 1, $P_{2000} = 0.09$) (Fig. 3). Over the course of the

Fig. 3. Annual and mean annual (span rate) survival rates, 95% confidence intervals, and probabilities from one-tailed binomial z tests for mule and white-tailed deer in south-central British Columbia, 1997–2000.
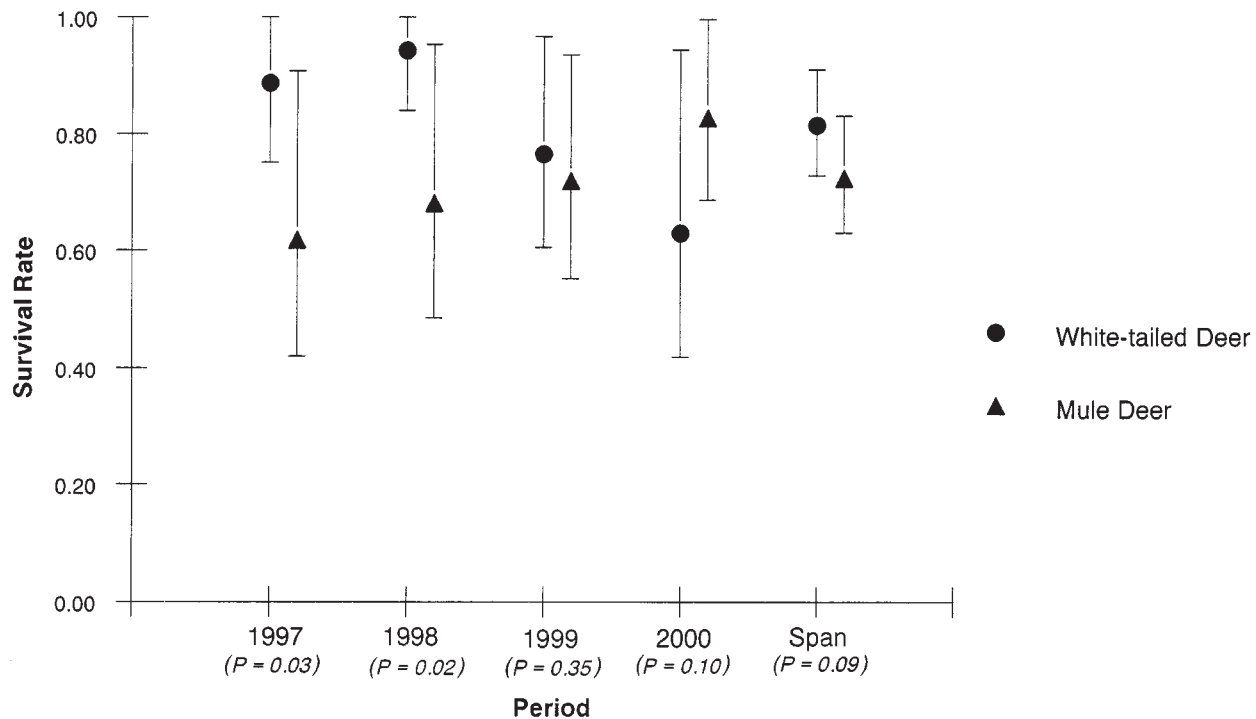
study, the annual adult mule deer survival rate ($S_{\mathrm{Span}} = 0.72$) was significantly lower than that for white-tailed deer ($S_{\mathrm{span}} = 0.81$) ($z_{\mathrm{span}} = 1.32$, df = 1, $P_{\mathrm{span}} = 0.09$) (Fig. 3), and there was a negative correlation ($R = -0.89$, $R^2 = 0.79$, $P = 0.11$) between the two.

The seasonal mule deer survival rate was lowest during winter ($S = 0.89$), whereas the white-tailed deer survival rate was lowest in spring ($S = 0.93$) (Fig. 4). Cougar predation was the predominant cause of mule deer mortality in all seasons except fall, when only unknown mortalities were recorded. Cougar predation was also the predominant cause of white-tailed deer mortality in all seasons except summer, when all mortalities recorded were classified as either vehicle-caused or unknown.

Determining cause-specific mortality rates 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 in two ways. First we censored unknown mortalities completely from the dataset. This resulted 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 white-tailed deer. Based on these data, we divided all mortalities into just 2 categories: predation (including cougar) and other (unknown mortalities were simply grouped with all other mortalities). This more conservative analysis showed that mule deer suffered significantly higher predation rates ($z = 1.57$, df = 1, $P = 0.06$) (Table 5).

Maternity

Mule deer does were checked for fetuses from 1997 to spring 2000. White-tailed deer does were examined only 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, $P = 0.44$).

Abundance and recruitment

An aerial survey conducted in February 2000 showed that white-tailed deer were almost three times more abundant (908 ± 152; mean $\pm$ SE) than mule deer (336 ± 122) within the study area. White-tailed deer recruitment (56 fawns : 100 does) was higher than mule deer recruitment (38 fawns : 100 does), though not significantly so ($\chi^2 = 0.9050$, df = 1, $P = 0.34$).

We observed fawn:doe ratios of 38:100 for mule deer and 56:100 for white-tailed deer. Based on these recruitment rates and the prepartum maternity rates discussed above, we estimated a fawn survival rate 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 that the fawn survival rate did not differ significantly from that in 2000, white-tailed deer showed a high growth rate following the hard winter of 1996–1997, then growth slowed significantly in 1999 and the population declined in 2000 (Fig. 5). Mule deer showed a lower initial growth rate that steadily increased to a positive growth level in 2000 (Fig. 5). However, based on this model over the course of the study, the mule deer population decreased annually by 12% ($\lambda = 0.88$), while the white-tailed deer population increased annually by 2% ($\lambda = 1.02$), with growth of the white-tailed deer popula-

Fig. 4. Seasonal cause-specific mortality rates for mule and white-tailed deer in south-central British Columbia, 1997–2000 (survival = 1 – total mortality).
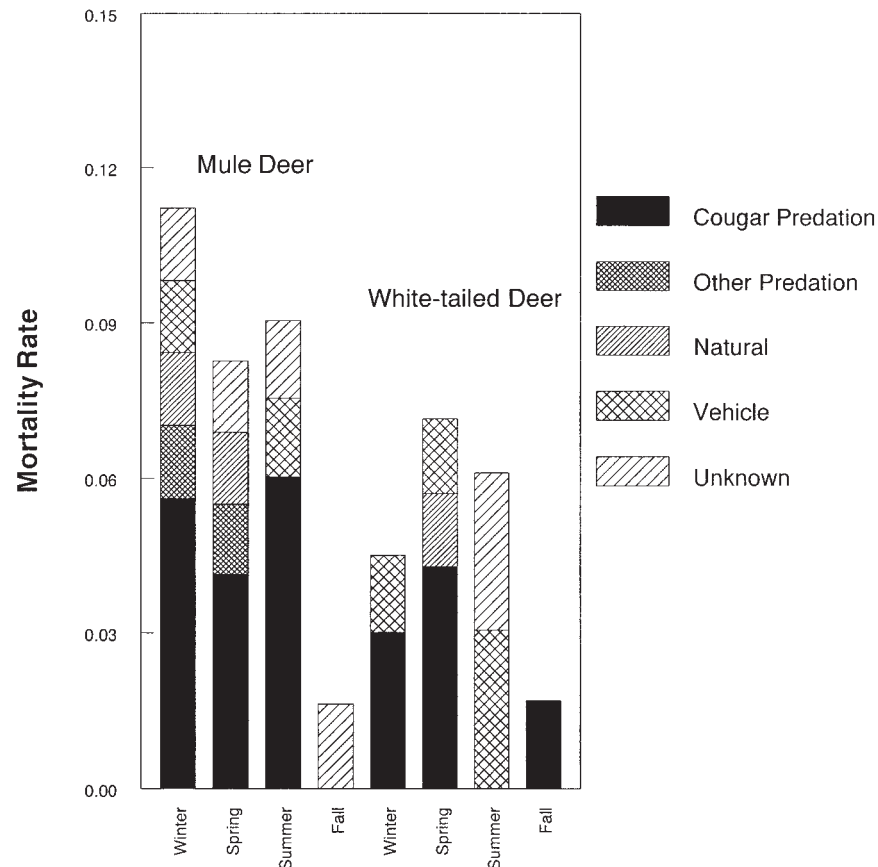
Table 4. Cause-specific mortality rates for mule deer and white-tailed deer in south-central British Columbia, 1997–2000 (unknown mortalities were censored from the data).

Cause of mortality	Mule deer mortality rate	White-tailed deer mortality rate	z score*	P
Cougar predation	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 rate	0.76 (0.00249)	0.84 (0.00198)	1.11	0.13

Note: Values in parentheses show the variance.
*One-tailed binomial z score.

tion in 1996 and 1997 countered by declines in 1999 and 2000. Both populations were most sensitive to changes in adult survival rates, the elasticity in the adult survival rate (0.83) being much higher than the elasticity in fecundity (0.17).

Density

Using harvest and hunter-effort records for both species we compared population trends over the previous 13 years (Fig. 6). The population trends for mule deer and white-tailed deer are positively correlated ($R = 0.62$, $R^2 = 0.38$, $P = 0.02$); however, while the white-tailed deer population showed a significant correlation between population trend and winter snow accumulation ($R = 0.58$, $R^2 = 0.34$, $P = 0.04$), the mule deer population did not ($R = 0.34$, $R^2 = 0.12$, $P = 0.26$).

Table 5. Cause-specific mortality rates for mule deer and white-tailed deer in south-central British Columbia, 1997–2000, using only two mortality classes, predation and other (unknowns are grouped with other).

| Cause of mortality	Mule deer mortality rate	White-tailed deer mortality rate	z score*	P
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 rate	0.72 (0.00261)	0.81 (0.00215)	1.32	0.09

Note: Values in parentheses show the variance.
*One-tailed binomial z score.

Fig. 5. 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.
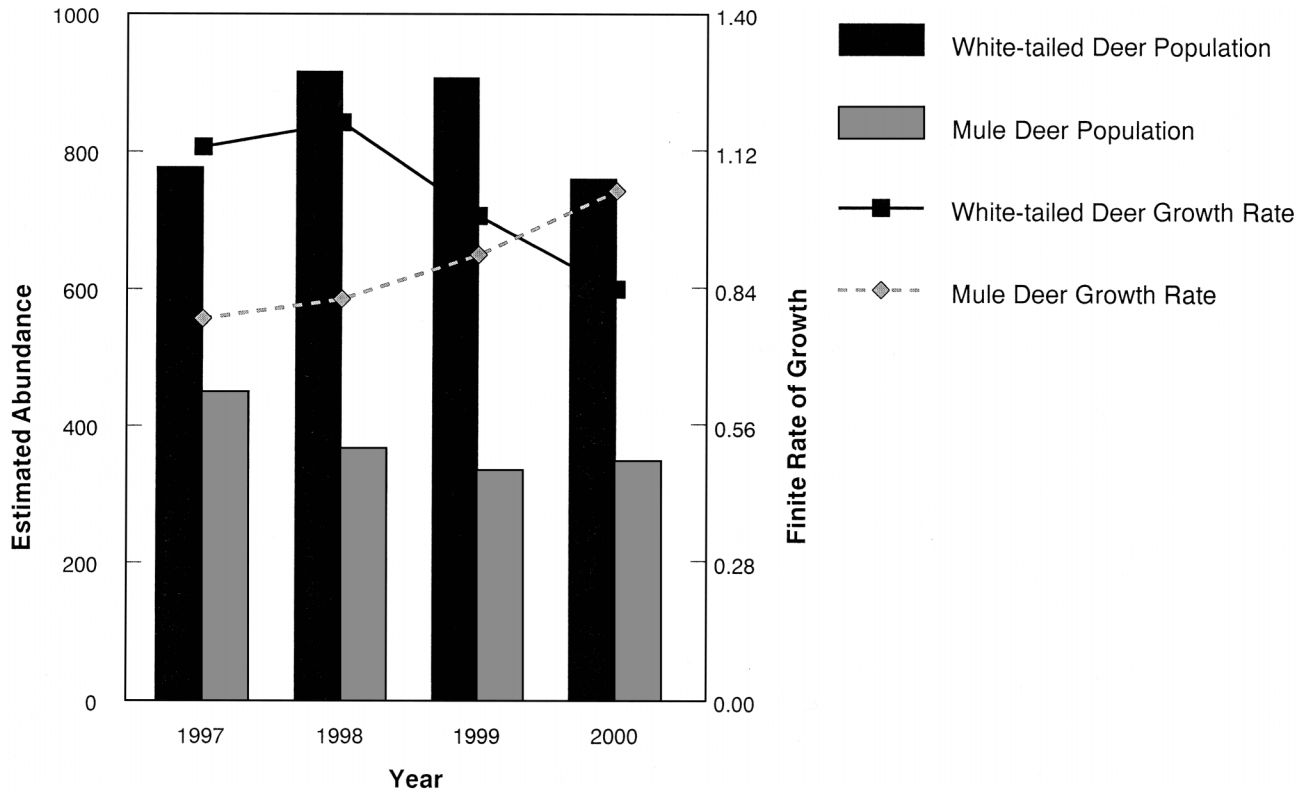
Fig. 6. Population index (number of deer harvested per unit hunter effort) for mule deer and white-tailed deer (British Columbia Ministry of Water, Lands and Air Protection, Cranbrook, unpublished data) in relation to snow accumulation (January–April), 1987–1999 (species-specific deer tags were not sold prior to 1987).
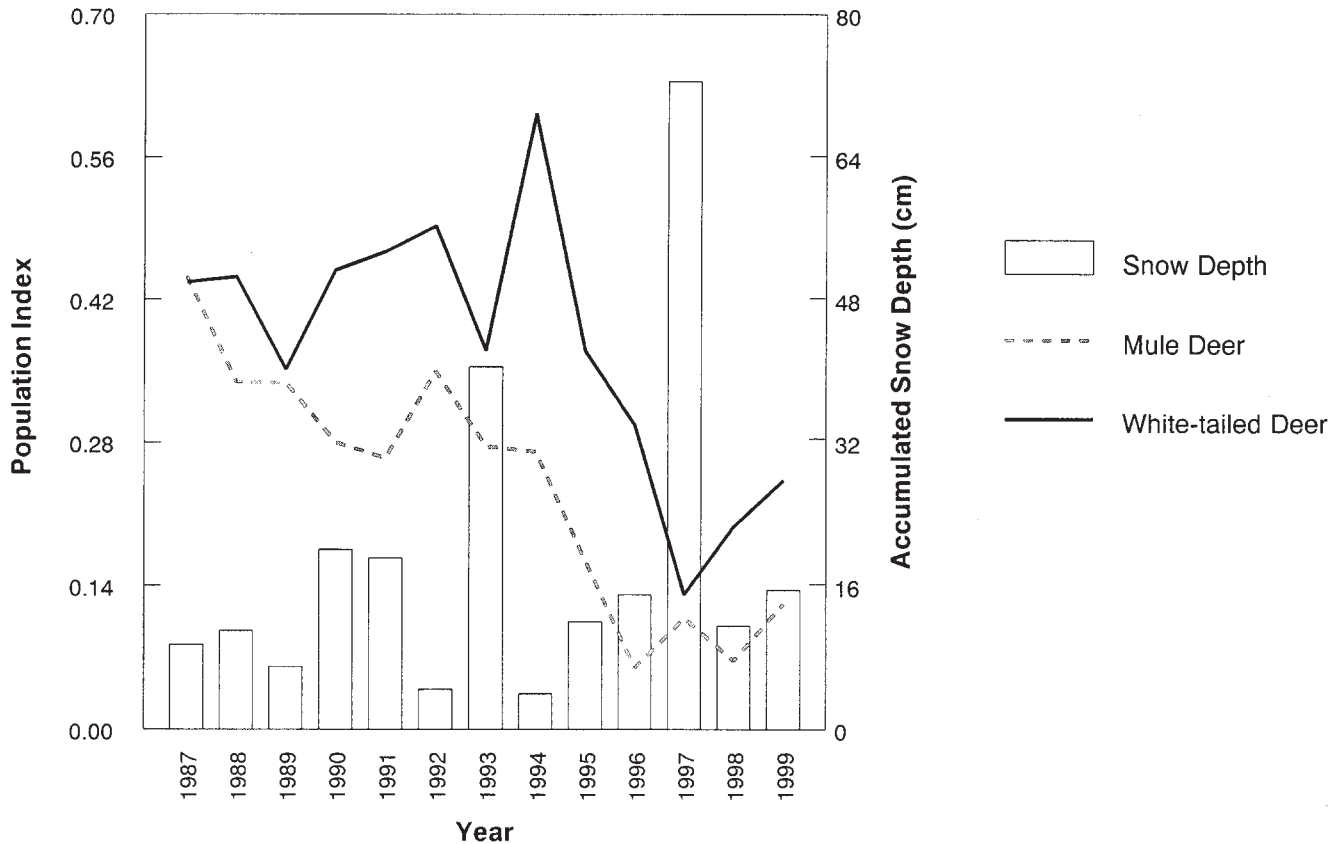
Fig. 7. Total predation rates and associated linear trend lines plotted against density of mule deer (solid line) and white-tailed deer (broken line) in south-central British Columbia, 1997–2000.
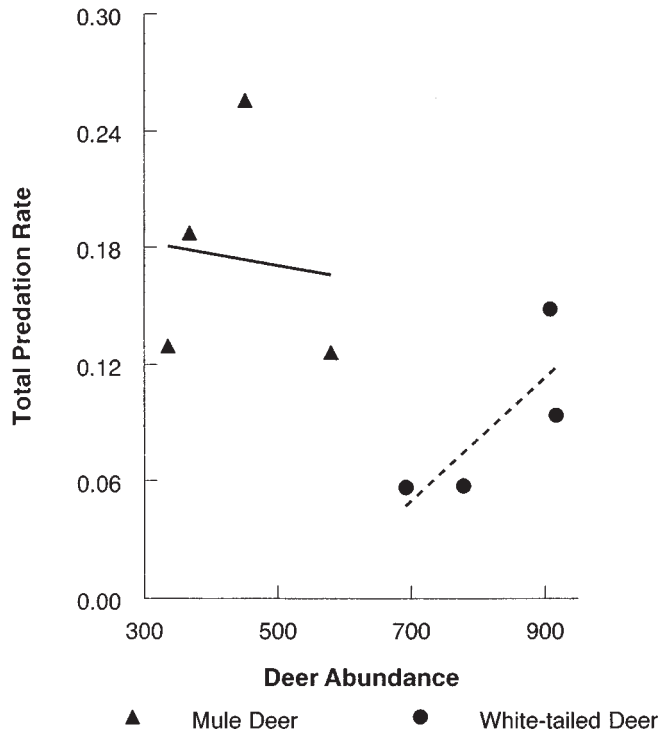
Further, the same pattern in population growth following the heavy snowfall of 1996–1997 documented during this study seemed to be repeated in 1992–1993 and 1988–1989.

Density-dependent versus density-independent predation

We plotted total predation rates against population densities estimated through the method discussed above (Fig. 7). The predation rate seemed to increase with prey density (density dependent) for white-tailed deer. By contrast, the predation rate seemed to increase (inversely density dependent) with decreasing prey density of mule deer.

Discussion

Overhunting 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. During the course of this study, humans 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 4-07 and 4-08, which make up our study area (British Columbia Ministry of Water, Lands and Air Protection, Cranbrook, unpublished data). This apparent discrepancy in our results may be due to the small number of males radio-collared (Table 1). Given that white-tailed deer were found to be three 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 rates or population sizes of these two species.

Stochastic-event hypothesis

Several researchers have documented high mortality rates

resulting from 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 rates in the first 2 years and last year of the study, and across the entire study period when all mortalities were pooled (Fig. 3). A comparison of the survival rates of both species (Fig. 3) also shows a negative correlation between the two ($R = -0.89$). Finally, the differences in survival rate were not caused by differences in mortalities attributable to malnutrition or starvation, which suggests that environmental stochastic events were not responsible for long-term declines in this mule deer population.

Limited resources/poor habitat hypothesis

Although our sample of maternity rates was small, the numbers found are very similar to rates reported in earlier studies with larger sample sizes in the same region. Just south of our study area, Zender (1987) found 1.74 fetuses per road-killed pregnant white-tailed deer ($n = 106$) compared with 1.83 in this study. Zeigler (1978) sampled 61 mule deer in central Washington State and counted 1.73 fetuses per doe compared with 1.78 in our area. Large variations are often seen in both species and are likely tied to differences in predominant habitat type (Mackie et al. 1998, p. 94). The habitats studied by Zender (1987) and Zeigler (1978) are 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 compared with those obtained in other studies. Mackie et al. (1998, p. 94) reported values ranging from 1.25 to 1.90 fawns per doe for mule deer and from 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 as indicated by femur marrow consistency. Only 1 of 13 white-tailed deer mortalities was classified as natural. The mule deer survival rate was lowest in winter, but cougar predation and not malnutrition posed the highest risk to mule deer during that season (Fig. 4). 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 femur marrow consistency. When combined, these factors (relatively high maternity rate and low mortality rate attributable to poor condition) suggest that this mule deer population's decline was not caused by limited food or habitat.

Predation hypothesis

The adult survival rate is the most important variable in the growth of any deer population (White and Bartmann

1997; sensitivity analysis in 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 population growth for both species. The predation rate was 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, the two species should have paralleled one another in population growth, with growth slowing as the populations increased, because of increased predation pressure. In the last 2 years of our study, population-growth rates deviated dramatically, with decreases in mule deer growth rates mirrored by increases in white-tailed deer growth rates (Fig. 5). The rate of predation on mule deer remained high throughout the study, regardless of mule deer density, but increased on white-tailed deer as that population rebounded from the severe winter of 1996–1997 (Fig. 7). Thus, predation appears to be density-independent or inversely density-dependent for mule deer and density-dependent for white-tailed deer.

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

Apparent competition

Apparent competition can occur at three spatial/temporal scales (Holt 1977; Holt and Lawton 1994). Predators may be supported by a single prey species, but during periods of low availability may switch to a secondary prey species (Hamlin et al. 1984; Sweitzer et al. 1997). Secondly, predators may move between habitats and encounter different prey (Seip 1992). Thirdly, invading prey may artificially inflate predator numbers, resulting in increased predation on resident alternative prey (Holt 1977; Pech et al. 1995; Namba et al. 1999; Sinclair et al. 1998, p. 569).

White-tailed deer populations are thought to be increasing across the West (Crête 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 (1977). Mule deer may therefore be at risk of depensatory predation, especially following perturbations in white-tailed deer densities (Sweitzer et al. 1997).

Traditional theory states that cougars are territorial predators which show a strong ability to regulate their own population (Seidensticker et al. 1973; Lindzey et al. 1994). Recent re-

search has suggested, however, that this may not hold and that cougars more strongly resemble a migratory generalist that responds to prey/deer densities (Pierce et al. 2000). Mobile predators, with short generation times, will respond most quickly to fluctuations in prey densities and therefore have a strong numerical response (Körpimaki and Norrdahl 1991). As generalist predators, cougars may show only a short time lag while adjusting their number to that of their primary prey. This time lag may be long enough to cause disproportionate predation on secondary prey (mule deer) but quick enough to allow primary prey (white-tailed deer) to quickly rebound to a high equilibrium.

The harvest data also seem to support the apparent-competition hypothesis (Fig. 7). 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 (1988–1989, 1992–1993, 1996–1997). 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 depensatory predation pressure, causing a further decline in the mule deer population until cougar densities adjust to the new white-tailed deer density. As predation on white-tailed deer is density-dependent, 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 Water, Land and Air Protection, Cranbrook, unpublished data), predation mortality of mule deer seemingly remained constant (13–19%) (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, immigrating 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 were unable to attain our sample goal of 40–50 animals of each species for each year. This reduction in radio-collared animals increases the variance of the rates associated with specific mortality causes and reduces the chance of detecting real differences between species (Type II error). 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.

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, Mass.

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.

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.

Ballard, W.B., Lutz, D., Keegan, T.W., Carpenter, L.H., and deVos, J.C., Jr. 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 Nat. **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. Manag. **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. pp. 1–10.

Caughley, G., and Sinclair, A.R.E. 1994. Wildlife ecology and management. Blackwell Science, Inc., Cambridge, Mass.

Cheatum, E.L. 1949. Bone marrow as an index of malnutrition in deer. N.Y. State Conserv. **3**: 19–22.

Clements, C.D., and Young, J.A. 1997. A viewpoint: rangeland health and mule deer habitat. J. Range Manag. **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. 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. Spec. Rep. Ser. 6, Research Branch, B.C. Ministry of Forests, Victoria. pp. 223–236.

Crête, 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. Hung. **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. Manag. **51**: 634–643.

Gill, R.B. 1999. Declining mule deer populations in Colorado: reasons and responses. Colorado Division of Wildlife, Denver.

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. Manag. **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, Athalmere, B.C.

Heisey, D.M., and Fuller, T.K. 1985. Evaluation of survival and cause-specific mortality rates using telemetry data. J. Wildl. Manag. **49**: 668–674.

Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. Theor. Popul. Biol. **12**: 197–229.

Holt, R.D., and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. Annu. Rev. Ecol. Syst. **25**: 495–520.

Ketcheson, M.V., Braumandl, 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. Spec. Rep. Ser. 6, Research Branch, B.C. Ministry of Forests, Victoria. pp. 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.

Körpimaki, E., and Norrdahl, K. 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. Ecology, **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. Manag. **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. Federal Aid Project W-120-R, Montana Fish, Wildlife and Parks, Helena.

McCorquodale, S.M. 1999. Movements, survival, and mortality of black-tailed deer in the Klickitat Basin of Washington. J. Wildl. Manag. **63**: 861–871.

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. pp. 967–984.

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.

McNay, R.S., and Voller, J.M. 1995. Mortality causes and survival estimates for adult female Columbian black-tailed deer. J. Wildl. Manag. **59**: 138–146.

Meidinger D., and Pojar, J. 1991. Ecosystems of British Columbia. Spec. Rep. Ser. 6, Research Branch, B.C. Ministry of Forests, Victoria.

Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. Ecology, **75**: 478–488.

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. Popul. Biol. **56**: 123–137.

Nelson, M.E., and Mech, L.D. 1986. Mortality of white-tailed deer in northeastern Minnesota. J. Wildl. Manag. **50**: 691–698.

O'Gara, B.W. 1978. Differential characteristics of predator kills. *In* Proceedings of the Eighth Biennial Pronghorn Antelope Workshop, Jasper, Alberta, 2–4 May 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. Manag. **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. Ecology, **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. Manag. **53**: 7–15.

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. 5th ed. Rev. The Wildlife Society, Bethesda, Md. pp. 324–348.

Roseberry, J.L., and Woolf, A. 1998. Habitat – population density relationships for white-tailed deer in Illinois. Wildl. Soc. Bull. **26**: 252–258.

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. Manag. **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. Manag. **56**: 718–725.

Sauer, J.R., and Williams, B.K. 1989. General procedures for testing hypotheses about survival or recovery rates. J. Wildl. Manag. **53**: 137–142.

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., and Pech, R.P. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos, **75**: 164–173.

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. Conserv. Biol. **12**: 564–575.

Solomon, M.E. 1949. The natural control of animal populations. J. Anim. Ecol. **18**: 1–35.

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. Conserv. Biol. **11**: 1407–1417.

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.

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. 2nd ed. Idaho Department of Fish and Game, Boise.

Unsworth, J.W., Pac, D.F., White, G.C., and Bartmann, R.M. 1999. Mule deer survival in Colorado, Idaho, and Montana. J. Wildl. Manag. **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 and Parks.

Woods, G.P. 1984. Habitat selection of white-tailed deer in the Pend d'Oreille Valley, British Columbia. M.S. thesis, University of Idaho, Moscow.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice Hall Inc., Englewood Cliffs, N.J.

Zeigler, D.L. 1978. The Okanogan mule deer. Bull. No. 15, Washington Department of Game Biology.

Zender, S. 1987. Summary of data collected on Stevens County road-killed white-tailed deer. Washington Fish and Game, Spokane Regional Office.