Evaluating Survival and Demography of a Bighorn Sheep (*Ovis canadensis*) Population

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Abstract: Having an understanding of how animal populations interact with their natural community is fundamental to wildlife management. In 1982 and 1983, pneumonia in southwestern Alberta's Yarrow-Castle bighorn sheep population resulted in a dramatic die-off, in which the population declined from approximately 400 sheep to fewer than 150. The population recovered to approximately 200 individuals by 1995, but a decline was observed in the proportion of ewes throughout the mid-1990s. We assessed the survival and demography of this bighorn sheep population using data from 46 radio-collared ewes from 2003 to 2005. Annual adult ewe ($\geq$2 years of age) survival estimates ranged from 0.83 ±0.07 to 0.90 ±0.06, and ewe survival did not differ significantly among years or core habitat areas, nor among seasons, or between probable causes of mortality. Annual lamb survival to ten months ranged from 0.41 ±0.01 to 0.54 ±0.02 over three years. The estimated reproductive rate among years (2003-2005) was 0.40 (95% CI: 0.29-0.55), with a recruitment (female lamb survival to 10 months) estimate that averaged 0.18 (95% CI: 0.12-0.27). Population growth rates fluctuate near 1.0, although recruitment appears low in comparison with other populations. We discuss possible factors influencing this bighorn sheep population and compare results to demographic patterns observed in other ungulate populations.

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A basic problem in population ecology is the identification and prediction of factors that affect population growth. However, without the collection of biological evidence, wildlife managers are left with a perplexing assortment of speculations. Predation, hunting, disease, weather, population density and natural food supply may all play roles in limiting wild game populations (Geist 1971, Murphy et al. 1990, Goodson et al. 1991, Jorgenson et al. 1997, Bergerud and Elliot 1998).

Long-term population trend data exists for many ungulate populations throughout North America, primarily attained through aerial census of unmarked individuals (Gonzalez-Voyer et al. 2001, Hamel et al. 2006). Wildlife managers rely on these surveys to mark trends in population dynamics (Festa-Bianchet 1992). However, when unexpected population changes are observed, distinguishing the causes through biannual trend surveys is almost impossible. Studies monitoring radio-collared individuals within a population are necessary for understanding which demographic variables are affecting population size (Gaillard et al. 1998). Identifying demographic markers in a population and managing on a herd-specific basis may be necessary.

Rocky Mountain bighorn sheep (*Ovis canadensis*) are specialized inhabitants of subalpine and alpine habitats. They tend to exist in small, sedentary, isolated populations with patchy distributions (Geist 1975, Risenhoover et al. 1988, Singer et al. 2000). They are habitat specialists preferring open grassy slopes for foraging in close proximity to steep rocky areas for escape terrain (Singer et al. 2000). Encroachment of conifers and shrubs as a result of fire suppression, have impacted sheep populations by limiting available habitat and restricting movement (Stelfox 1976, Risenhoover et al. 1988, Singer et al. 2000). Bighorn sheep are subject to fluctuations in population size due to a number of factors but the effects of disease on bighorn sheep populations are particularly dramatic, leading to significant die-offs (Singer et al. 2000, Cassirer and Sinclair 2007).

Bi-annual winter aerial census surveys in the Yarrow-Castle area of Alberta, Canada indicated an increase in the bighorn population during the 1970s to approximately 400 individuals (Clark and Bergman 2005). During 1982 and 1983, pneumonia caused this population to decline to less than 150 animals (Onderka and Wishart 1984). The trend from 1985 to 1993 reveals steady population growth, at an increasing rate of approximately 10% per year. However, it appears that population recovery ceased in the mid-1990s, leveling off to current numbers of 200 to 250 sheep. A general decline in the number of bighorn ewes after 1993 was observed from aerial census counts (Clark and Bergman 2005). Reasons for the decline in ewe numbers are unclear due to lack of data beyond the regular aerial census surveys.

The purpose of this study was to gain an improved understanding of factors that may limit ewe numbers in the Yarrow-Castle region. Specific objectives were to: 1) quantify survival of radio-collared ewes and their lambs, 2) assess causes of mortality of radio-collared ewes, 3) calculate radio-collared ewe reproductive rates, and 4) estimate population growth. We tested for effects of year, core area residency, season, and probable cause of mortality on adult ewe survival. If adult ewe survival was limiting, we wanted to determine if it was due to a single type of mortality effect. We estimated reproductive rates and lamb survival by monitoring the radio-collared ewe population. Population growth was estimated by combining the survival and reproductive rates. By comparing our results to other studies, we could begin to determine which factors may have the greatest influence on the Yarrow-Castle population.

Methods

Study area

The study was conducted in a 450 km^2 area, located along the front ranges of southwestern Alberta, Canada, approximately 30 km southwest of the town of Pincher Creek (49°29'N, 113°57'W). The most southerly portion of the study area borders the northern boundary of Waterton Lakes National Park, while river drainages and forest create the northern and western boundaries, and foothill and prairie habitat create the eastern boundary.

The Yarrow-Castle area is situated in the Rocky Mountain and Foothill natural regions of southern Alberta. Bighorn sheep predominantly use the subalpine and alpine sub-regions ranging in elevation from 1550 m to 2600 m. Vegetation patterns are largely influenced by elevation, topography, aspect and wind exposure. Krummholz subalpine fir (*Abies lasiocarpa*) and whitebark pine (*Pinus albicaulis*) dominate the treeline while open stands of Engelmann spruce (*Picea engelmannii*), subalpine fir, subalpine larch (*Larix lyallii*), limber pine (*Pinus flexilis*), lodgepole pine (*Pinus contorta*) and aspen (*Populus tremuloides*) are found at lower elevations. Rock faces, open scree slopes, and herb-rich grassy meadows are located throughout, while recurring Chinook winds produce snow-free phases during the winter. Winds of 100 km/hr are not uncommon. The area receives annual average precipitation of 1054 mm with annual temperature averaging -1.33 °C (source data: Alberta Environment, Spionkop Creek climate station daily air temperature and precipitation summary data, 1984-2004).

Potential predators of bighorn sheep in the Yarrow-Castle area include grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), cougar *(Puma concolor*), wolverine (*Gulo gulo*), wolf (*Canis lupus*), coyote (*Canis latrans*), bald eagle (*Haliaeetus leucocephalus*) and golden eagle (*Aquila chrysaetos*). The area also supports a diversity of other big game species including elk (*Cervus elaphus*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), and mountain goat (*Oreamnos americanus*). Petroleum and natural gas developments, roadways, domestic grazing and controlled recreational activities occur in the study area. Motorized access in the area is controlled via locked gates and/or timing restrictions.

Capture and monitoring

We captured most ewes by net-gunning from the air using a helicopter during winter months, while a small number of individuals were captured during summer months using a clover trap (Clover 1954) baited with salt. Ewes were fitted with a very high frequency (VHF; 500 model, Telonics Inc., Mesa, Arizona) or global positioning system (GPS; 4000 model, Lotek Wireless Inc., Newmarket, Ontario) collar. Collars were affixed with a length of coloured rubber and engraved with a unique symbol allowing for individual identification in the field. Collars were fit on all captured ewes but biological data was only recorded if the animal did not appear to be overly stressed (breathing rate did not increase while processing). Horn measurements (total length, basal length and annuli lengths), age (determined by counting horn annuli), and body measurements (length and girth) were recorded.

From 2002 to 2005, 46 bighorn ewes were captured and radio-collared throughout the Yarrow-Castle study area. Thirty ewes were captured during December 2002, three in June 2003, twelve in January 2004, and one in January 2005. Ewe age at capture ranged between two and eight years, with an average of five (53% were <5 years of age).

Ground monitoring consisted of driving accessible roads and other access points and listening for radio collar signals using a hand-held telemetry receiver (R-1000 model, Communications Specialists Inc., Orange, California) and either a portable H-antenna or a truck-mounted omni antenna, both by Telonics. Ground monitoring was conducted weekly to ensure the best chances of finding fresh evidence for determining cause and approximate day of death for radio-collared ewe mortalities. We were not always able to conduct a weekly relocation for every individual for the entire year due to ewe location, collar complication or staff availability. Radio collars were equipped with 4- and 8-hour delay mortality sensors for GPS and VHF collars, respectively.

Lamb status

During the initial weeks of lambing, we visually determined the lambing status of radio-collared ewes on a daily basis, or as frequently as feasible to minimize chances of missing lambs. Since birthing events occurred over the entire range and staff availability was limited, our lambing observation attempts were sometimes spaced 2 to 5 days apart. For this study, lambing period was defined as starting at the latter part of May and progressing to mid-July (Festa-Bianchet 1988*c*). Ewes often moved into rugged, secluded terrain during lambing, which then required aerial observations to locate birthing events. After the lambing period, lamb survival was monitored by conducting bi-monthly observations until the lambs neared ten months of age. The final observations in March were typically re-evaluated, or required longer observation times, since the lambs tended to stray from their mothers for short periods but still associated with them by travelling, feeding (including occasional suckling attempts), or bedding down near them. The period in which weaning occurs is often indistinct (Festa-Bianchet 1988*d*) since young will still attempt suckling even once they are obtaining their nutritional needs from vegetation (Festa-Bianchet et al. 1994). However, October has been identified as the approximate time that bighorn wean (Festa-Bianchet et al. 1995). Since our lamb population was not collared or tagged, there is a possibility that lambs remained on their own once weaned from their mothers and their survival status mistakenly identified during final observations in March.

Survival rates

To ensure assumptions associated with calculating survivorship rates were met (Erickson et al. 2001), we addressed three that were relevant to our study. First, although radio-collared ewes were typically verified as alive or dead on a weekly basis, we consistently monitored individuals at least monthly, and therefore use a 30 day interval in the survival analysis. Lapses in our weekly observations were typically a result of logistical challenges with remote ewes, collar performance, or staff availability. We were able to determine the fates of all radio-collared ewes and all ewes were located at least once every month over the course of the entire study period. Second, during 2004 and 2005, 12 GPS collars were placed on ewes throughout the study area. The GPS collars were programmed to begin drop-off by September 2005. Due to drop-off timing, 10 of the 12 GPS-collared ewes were removed from any survival analysis since we were unable to determine their survival status to the end of the 2005 annual period or to the end of the field monitoring period which was April 2006. This eliminated effects of non-random censoring in the sample (Tsai et al. 1999, Garshelis et al. 2005). The remaining two GPS-collared individuals died prior to their collars' scheduled drop-off date and were included in the survival analysis. Third, aging ewes based on horn annuli is accurate only until about four years of age (Geist 1966). Therefore, we pooled data into one class of adult ewes to calculate survival (ewes $\geq$2 years of age).

One additional ewe was originally radio-collared within the study area but was clearly not a permanent resident of the Yarrow-Castle bighorn population. This ewe immediately returned to an area approximately 15 km southwest of the Yarrow-Castle and continued to inhabit that area for the remainder of the study and therefore was not included in our analysis. We estimated adult ewe survival rates from 33 VHF radio-collared ewes and two GPS-collared ewes. The 35 ewes were monitored for an average of 30 months each (min. 1.4, max. 40.7 months). Each study year consisted of a similar number of marked individuals (ewes at risk) within the survival samples.

Adult ewe survival rates were estimated using the Kaplan-Meier survival estimator, incorporating the staggered entry design (Pollock et al. 1989). The staggered entry design allowed for animals to enter the analysis at different times, assuming that new animals have the same chance of survival as previously tagged animals. We used the program Ecological Methodology Version 6.1.1. (Kenney and Krebs 2003) to perform the computations to estimate survival (Krebs 1999).

We examined survival rates based on four factors: 1) year, 2) core area residency, 3) season, and 4) mortality type. We assumed that 3 years of data would detect variance in survival rates but acknowledge this limited time span is minimal for long lived species. We calculated survival estimates separately for each year and tested for yearly differences using a log-rank test (Garshelis et al. 2005) within the Ecological Methodology program (Kenney and Krebs 2003).

We examined whether survival rates differed among Yarrow-Castle ewes that occupied different core areas. Ewe's could be more susceptible to mortality in some areas due to higher predator loads associated with an alternative prey base, specialized predators, forest encroachment or risks associated with moving among habitat patches to acquire their dietary needs. We identified core areas by creating 60% fixed kernel polygons using the GPS collar data. We assumed that the GPS-collared individuals represented range-use of all ewes within the study area. We used the program HRE: Home Range Extension for ArcView® (Rodgers and Carr 1998) to calculate 60% kernel polygons to represent ewe core range as opposed to a 50% value (Girard et al. 2002), because at 60% partial polygons within the identified core ranges were eliminated. Both VHF- and GPS-collared ewes were assigned to an identified core range within the study area. Survival estimates for core residency were conducted by pooling yearly survival for each core area, and comparing cumulative survival among core areas using log-rank tests.

We defined seasonal time periods using the elevation data collected by the GPS collars. Generally four seasonal divisions are recognized in temperate regions but since bighorn ewes utilize only two to three distinct seasonal ranges throughout the year, (Geist 1971:1975, Festa-Bianchet 1988*a*) we used seasonal migration to define season. Sheep will make altitudinal migrations throughout their range to exploit vegetation high in quality and availability (Geist 1971, Seip and Bunnell 1985). We calculated the mean daily elevation across all GPS-collared ewes for the entire study area over all years (2003-2005). We visually interpreted the graphic produced by plotting daily elevation averages to determine the dates for seasonal periods. Three seasonal periods were identified: winter (15 December-25 May), summer (26 May-23 August), and fall (24 August-14 December). We calculated survival rates for each seasonal time period among years and compared survival estimates among those time periods using log-rank tests.

Lastly, we wanted to determine if predator mortality affected ewe survival differently from non-predator mortality in the Yarrow-Castle area. As such, we compared predator mortality vs. non-predator mortality by estimating survival while factoring in one mortality type (e.g., predator mortality) and censoring deaths from the other type (e.g., non-predator mortality; Garshelis et al. 2005). We acknowledge that compensatory mortality could occur when a predator targets a weakened individual that would have otherwise been categorized as non-predator type mortality. Moreover, we may also misclassify mortality types if a dead carcass is scavenged by a predator but died from other causes. Nonetheless, we were interested in determining whether adult ewe mortality was primarily linked to predation. Predator mortalities were typically comprised of piled remains of sheared hair, broken bones and an opened skull. The non-predator mortalities consisted of whole or almost whole carcasses, but often fed upon by birds and insects. Carcass remains were occasionally examined by a qualified veterinarian to help determine cause of death. We used a log-rank test to assess if ewe survival was influenced by one type of mortality more than the other.

Lamb survival to ten months of age was estimated using the following formula: $1 - (\sum d_i / \sum b_i)$, where d is death of a lamb, and b is birth of a lamb from each ewe i. Only lambs of radio-collared adult ewes were considered in the survival estimates. A female that was never observed with a lamb by mid-July, was accepted as not lambing that year. We considered orphaned lambs (lambs of ewes that died during the months of June through early September) as mortalities, since they would not be fully weaned from their mothers and were likely still dependent on maternal care (Festa-Bianchet et al. 1994). Each female that was confirmed having a lamb was monitored bi-monthly to determine lamb survival until late winter. In March, a final lamb count for radio-collared ewes determined the total number of lambs surviving to approximately ten months of age. A log-rank test determined if lamb survival differed among years based on a summer (May-November) and winter (December-March) lamb season since high summer lamb mortality may indicate sporadic pneumonia (Cassirer and Sinclair 2007).

Reproductive rates

All radio-collared ewes were considered reproductively mature at capture. Ewes can reproduce at two years of age (Jorgenson et al. 1993*a*, Festa-Bianchet et al. 1994) and generally remain reproductive until about 14 years (Bérubé et al. 1999). Previous work has shown that ewes rarely twin (Geist 1971, Eccles and Shackleton 1979), and thus we assumed litter size to be 1. The lamb status of each ewe determined yearly reproductive success for each individual, although some ewes were not included in reproductive analysis if they did not survive to their first monitored lambing period, or if their GPS collars had dropped before their lamb was ten months of age.

We estimated the reproductive rate for the Yarrow-Castle ewe population from field data of 41 radio-collared ewes. In total, we observed 91 ewe-years of reproduction. Only two radio-collared ewes were two years of age during capture and neither ewe was lactating at the time. All radio-collared 3-year-olds were recorded as lambing. We calculated inter-birth intervals (the variability in lifetime reproductive success) in two ways, lamb produced and lamb surviving. We examined each ewe’s reproductive record chronologically and tallied the number of years from the production of a lamb (or lamb surviving) to the production of the next lamb (or lamb surviving). We calculated the mean interval between lambs (or lamb surviving) across all ewes. In the producing column of the birth interval table (Appendix A), a one represented a ewe having a lamb every year during the study period, and a two meant that a ewe was producing a lamb every other year during the study period. A one in the surviving column represented a ewe whose lambs all survived to ten months, while a two meant the ewe had lost a lamb amid two successful observation years.

A reproductive rate was calculated for each ewe that produced a lamb whether it survived or not, and a recruitment rate was calculated for each ewe that produced a lamb that survived to ten months of age. We constructed two spreadsheets similar to those used by Garshelis et al. (2005). The spreadsheet for annual reproductive estimation incorporated columns that represented the reproductive history (production of a lamb) for each year (2003-

2005), and rows that represented individual ewe reproduction (Appendix B). Each ewe was assigned a number during each reproductive year she was observed. A cell with a 0, represented a year in which a ewe did not lamb, a cell with a one represented a ewe that produced a surviving lamb to ten months, while a grey cell with a one (or a grey cell with a 0 when referring to the recruitment table), represented a ewe that produced a lamb but the lamb did not survive to ten months. Annual reproductive rates were calculated by dividing the total number of female lambs born (produced) that year, by the total number of ewes observed that year. Individual reproductive rates were calculated by dividing the total number of female lambs born (produced) to each ewe (assumed that 50% of lambs born were female) by the number of years the ewe was observed. A recruitment rate was calculated by dividing the total number of female lambs born and surviving to ten months by the total number of observed ewe years over the study period (Appendix C). Confidence intervals for reproductive and recruitment rates were determined by calculating confidence limits for proportions based on a method equivalent to the ratio of *F* distributions (Zar 1984) and then calculating into an odds ratio, representing a lamb/ewe ratio.

Population growth rates

We estimated population growth rate (λ) for two scenarios using a female based, age structured, deterministic Leslie matrix (Leslie 1945, Caswell 2001). Our first approach incorporated two age classes based on our data (lamb and adult ewe≥ 2 years of age), assuming yearling survival (1-2 years) was 100%. Bighorn yearlings have been found to occasionally experience 100% survival (Jorgenson et al. 1997). For our second approach, we used our data in association with three hypothetical estimates for yearling survival, based around yearling survival rates from other studies (Jorgenson et al. 1997, Loison et al. 1999, Gaillard et al. 2000). First, an average of the Yarrow-Castle adult survival estimate represented an upper limit for yearling survival. Second, an average of the Yarrow-Castle lamb survival estimate represented a lower limit for yearling survival while a midpoint of the upper and lower survival rates was used to represent a third yearling survival rate in the 3-stage matrices. We conducted both 2- and 3-stage (incorporating the yearling age class) matrix analyses for each study year (2003-2005) and compared the resulting λ estimates. Population growth estimates were calculated from the matrices using the excel software extension, PopTools (Hood 2006).

Results

Eleven radio-collared ewes died during the monitoring period with an average ewe lifespan of 6.87 years. Annual adult ewe (ewes≥2 years of age) survival ranged from 0.83 to 0.90 over three years (Table 1). We did not find evidence that survival differed among years (2003 vs. 2004: χ^2 = 0.60, df = 1, P = 0.44; 2003 vs. 2005: χ^2 = 0.37, df = 1, P = 0.54; 2004 vs. 2005: χ^2 = 0.02, df = 1, P <0.995). Three core bighorn ewe territories were identified within the study area: a southern, a central, and a northern core. Ewes occupying the southern core experienced the lowest cumulative survival rate (Table 1). The southern core experienced several mortalities and had a lower survival estimate, but ewe survival among core areas was not significantly different (southern vs. central core area: χ^2 = 1.38, df = 1, P = 0.24; southern vs. northern core area: χ^2 = 1.05, df = 1, P = 0.31; and central vs. northern core area: χ^2 = 0.00, df = 1, P <0.995). Cumulative survival estimates were calculated for each seasonal period with the fall season having the greatest survival (Table 1), yet survival among seasons was not significantly different (winter vs. summer: χ^2 = 0.00, df = 1, P = <0.995; winter vs. fall: χ^2 = 2.28, df = 1, P = 0.13; summer vs. fall: χ^2 = 2.35, df = 1, P = 0.13).

Of 11 ewe mortalities, the evidence for seven suggested predators as the most likely cause, while four were non-predator related. Of the seven probable predator mortalities, four had evidence to suggest cougar kills, two from bear, and one from wolverine. Four non-predator mortalities consisted of one fall, one avalanche, one unknown, and one originating from a broken leg. Although cumulative ewe survival based on predator mortality type was lower than non-predator (Table 1), ewe survival did not differ significantly between mortality types (predator vs. non-predator: χ^2 = 0.82, df = 1, P = 0.37).

The majority of Yarrow-Castle lambs were born during the initial weeks of June and we did not observe any twinning during our study. Annual lamb survival ranged from 0.41 to 0.54 over three years (Table 2). The lambing rate was lower in 2004 (65%) when compared to 2003 and 2005, but lamb survival was greatest that year (54%). Although 2004 had the greatest lamb survival rate, it also had a higher occurrence of winter lamb mortality when compared to summer mortality. The lamb population suffered greater mortality during the winter seasons of 2004 (64% winter mortality) and 2005 (77% winter mortality); However, during 2003, the lamb population suffered equal mortality (50%) during the seasons. Lamb survival did not differ significantly between summer and winter season among years (2003 vs. 2004: χ^2 = 0.81, df = 1, P = 0.37; 2003 vs. 2005: χ^2 = 0.12, df = 1, P = 0.73; 2004 vs. 2005: χ^2 = 0.31, df = 1, P = 0.58).

Radio-collared ewes produced lambs on average every 1.3 years over the 3-year period. However, this interval increased to every 1.7 years for a radio-collared ewe that had to produce a lamb that survived to ten months of age (Appendix A). Based on these intervals, incorporating an average ewe lifespan of 6.87 years (average ewe age of the 11 radio-collared Yarrow-Castle ewe mortalities), a ewe will give birth to 2.93 lambs, of which 2.32 lambs will survive to ten months if primiparous at age three. All 3-year-olds in our study were recorded with lamb therefore the ewes have approximately 4 reproductive years on average. The overall reproductive rate (female lambs produced per ewe) was 0.40 (95% CI: 0.29-0.55). We observed reproductive rates of 0.47 (95% CI: 0.27-0.82), 0.32 (95% CI: 0.19-0.56), and 0.44 (95% CI: 0.24-0.81) female lambs/ewe for 2003, 2004, and 2005, respectively (Appendix B). An overall recruitment rate of 0.18 (95% CI: 0.12-0.27) was calculated for female lambs surviving into the population to ten months of age (Appendix C). Annual recruitment ranged from 0.18 to 0.19.

Annual estimates of λ based on the 2-age class matrix with yearling survival of 100% resulted in positive growth rates (1.018-1.064; Table 3). The λ estimates based on the 3-age class matrices (incorporating yearling survival of 87%, 66%, and 45%) were predictably lower. Population growth was negative for all 3-age class matrices during 2003 (0.930-0.997) and during all years when incorporating the low yearling survival rate of 45% (0.930-0.982; Table 3).

Discussion

Disease had played a prominent role in limiting the Yarrow-Castle bighorn sheep population in the early 1980s, and while disease no longer appears to be a factor, the population appears limited in some way.

Monitoring the radio-collared ewes allowed us to estimate survival and reproductive rates, as well as estimate population growth. It is difficult to detect sampling, yearly or environmental variance with only three years of data for a long-lived species but we assume that our estimates are representative for a longer period and compare our results with other bighorn populations within North America.

Adult female survival

Survival rates of adult female bighorn sheep vary across North America. Singer et al. (2000) found stable or increasing bighorn herds in the western United States having a combined-ewe age survival rate of 0.89, while populations suffering from active epizootics had a combined-age ewe survival rate of 0.67. In Alberta, Loison et al. (1999) found mean prime age (3-7 years) ewe annual survival rates ranged from 0.92 to 0.94 and Jorgenson et al. (1997) reported senescent (8+ years) ewe survival of 0.85. Our estimates of mean ewe survival rates are lower than those comparables, but our confidence intervals overlap with these rates from other areas. Our annual survival estimates include older ewes which typically experience lower survival than younger adult ewes (Jorgenson et al. 1997, Loison et al. 1999), which may account for these differences. We expect that our limited time span of data collection may affect the precision of our estimates.

Overall, adult ewe survival should be relatively stable with little variation among years (Gaillard et al. 1998, Loison et al. 1999). Changes in adult ewe survival may severely affect a population's growth rate, in particular prime-aged ewe survival (Gaillard et al. 2000). Our data did show yearly variation in the means from 0.83 to 0.90. The lower survival rate in 2003 (0.83) could be attributed to higher mortality in the southern core area that year due to predation but this appeared to be a 1-year event and if we consider the last two years only, ewe survival was more stable.

The Yarrow-Castle area supports at least three distinct core ewe groups. Ewe survival was low in the southern core during 2003, but because there was no significant difference in survival rates among the three core groups, we concluded that no one core group was driving overall survival. The southern core had a larger number of ewes at risk (radio-collared) when compared to the other two cores, therefore creating relatively equal survival among core areas.

Bighorn sheep generally occupy more than one range among seasons (MacCallum and Geist 1992, Alberta Environmental Protection 1993). Rams can experience lower survival in the fall due to the additional cost of participating in the rut (Festa-Bianchet 1987, Jorgenson et al. 1997), but reproduction does not appear to negatively affect female survival (Jorgenson et al. 1997). Seasonal difference in survival rates have been reported for other ungulate species, largely climate related (dall sheep *Ovis dalli*, Burles and Hoefs 1984; caribou *Rangifer tarandus caribou*, McLoughlin et al. 2003; and alpine ibex *Capra ibex*, Jacobson et al. 2004). Although the bulk of our ewe mortalities occurred between March and July, survival rates were not significantly different among seasons.

Predator-caused ewe mortality was slightly higher than non-predator related deaths in this study. It is possible that our predator related mortality is overestimated since many predators are also known to scavenge carcasses (Bauer et al. 2005, Green et al. 1997, Hornocker and Hash 1981, Landa et al. 1997, Mattson 1997, van Zyll de Jong 1975). During this study, cougar had caused the majority of predator related mortality. Cougars preying primarily on sheep can have a significant local impact on bighorn populations (Ross et al. 1997, Réale and Festa-Bianchet 2003). Bouts of cougar predation on bighorn sheep are known to last between three to five years and are associated with a noticeable decline in adult survival, in some cases dominating population dynamics (Festa-Bianchet et al. 2006). Initially, we were concerned that the southern core area bordering Waterton National Park could be a mainstay for cougar specializing in bighorn sheep, but according to the Cougar Management Guidelines Working Group (2005), a predator pit (Hayes et al. 2000) does not exist unless the prey species is in excellent physical condition and the population is experiencing high fecundity. Despite this, the study area bordering the park boundary supports several additional prey species such as mule deer, white-tailed deer, moose, elk, and mountain goat. Thus a predator pit could exist, but bighorn predation rates could also vary among years as the predators change between alternative prey species (Jorgenson et al. 1997).

Yarrow-Castle ewes suffered from non-predator caused mortalities. Some climbing deaths have been reported in bighorn sheep during the rutting season (Festa-Bianchet 1987) and also shortly after translocations (Kamler et al. 2003). Twenty-two percent of the Hells Canyon bighorn sheep metapopulation suffered from falls or injuries (Cassirer and Sinclair 2007), while sporadic disease was the primary source of adult mortality. Sporadic pneumonia-caused mortalities in both adults and lambs were the primary factor limiting population growth and yet, these were not catastrophic outbreaks (Cassirer and Sinclair 2007). Further investigation is required to determine if there is some underlying factor (e.g., disease) making Yarrow-Castle ewes susceptible to non-predator caused mortality, or if it is occurring by chance. Moreover, Yarrow-Castle ewes were not harvested, either legally or illegally, during the study period (2003-2005). However, during the winter of 2006/2007, three rams and two ewes were confirmed to be poached on two separate occasions within the Yarrow-Castle study area. The extent to which poaching is affecting the Yarrow-Castle bighorn population is unknown, but to the best of our knowledge, these were the first recorded sheep poaching incidents within the Yarrow-Castle area.

Lamb survival

Lamb survival in our area may be low in comparison to estimates in other areas (Festa-Bianchet 1988*b*, 1988*c*, Gaillard et al. 1998, Singer et al. 2000). In the western United States, stable or increasing bighorn populations experienced an average lamb (0-1 year) survival rate of 0.65, while declining herds reached only 0.21 (Singer et al. 2000). In a Alberta bighorn population, lamb survival to weaning (approximately 5 months of age) ranged from 0.53 to 0.87 (Festa-Bianchet 1988*c*) while juvenile survival (0-2 years of age) ranged from 0.39 to 0.48 (Gaillard et al. 1998). Our lamb survival (to 10 months of age) ranged from 0.41 to 0.54. Due to our limitations in detecting neonatal lamb mortalities and early mortalities that could have occurred before first visual confirmation, our lamb survival estimates could be overestimated. Furthermore, since lambs were not radio-collared or marked in any way, we can not be certain that a radio-collared ewe's lamb was actually dead during our final lamb survival observations.

During 2004 the Yarrow-Castle lambing season was delayed. Fewer lambs were born during that year when compared to the other two years, yet lamb survival was highest that year. On the contrary, Festa-Bianchet (1988*a*) found lamb survival to decrease with prolonged birthdates. Lambs born in May experienced higher survival rates (survival to 1-year) that ranged from 0.19 to 0.68, while lambs born in June and July experienced survival rates that ranged between 0.11 and 0.33 (Festa-Bianchet 1988*b*). Portier et al. (1998) discovered neonatal survival to be higher in years with wet and warm springs, increasing maternal nutrition, as well as the quality and quantity of vegetation available to the lamb. According to Alberta Environment's climate data from Spionkop Canyon (within the southern core), the spring of 2004 was unusually wet and cool in the Yarrow-Castle area. Precipitation during April, May, and June 2004 were all higher than the 20-year averages for these months. The highest recorded monthly precipitation occurred during 2004 at 222 mm, when the monthly average was only 95 mm. Therefore, the wet spring may be associated with higher lamb survival that year. Cooler temperatures were also recorded for April, May, and June 2004 when compared to the 20-year monthly averages. May had the coldest recorded monthly average temperature at -7.16 °C while the 20-year average for May was +1.69 °C. Perhaps during 2004, being born late was more beneficial due to the cool temperatures that early born lambs would have had to contend with. The cooler temperatures and high precipitation levels would have also resulted in a later growing season that allowed these late born lambs to better survive. Alternatively, the 2004 lamb survival rate may reflect the fact that a number of lambs died shortly after birth, but were not detected.

Yarrow-Castle lamb survival was compared between the summer and winter seasons. Using 20 years of lamb mortality data, Portier et al. (1998) found summer mortality to be low, averaging 8% per year, compared to neonatal mortality rates of 17%, and winter mortality of 28%. Singer et al. (2000) established that summer lamb mortality was higher in declining or suspected diseased bighorn populations, than in populations that were increasing. Cassirer and Sinclair (2007) also found that summer lamb mortality was greater than 50% when sporadic pneumonia was the cause of death, with most mortalities occurring between six and ten weeks. Summer lamb mortality in the Yarrow-Castle area was 50%, 36% and 23% for 2003, 2004, and 2005, respectively. Our summer lamb mortality rates were higher than the 8% reported by Portier et al. (1998), but according to Singer et al. (2000) and Cassirer and Sinclair (2007), these higher summer lamb mortality rates could be indicative of a population limitation.

Reproduction

Our lifetime reproductive success is lower than that observed by Festa-Bianchet and Jorgenson (1996), where they found ewes producing an average of 7.09 and 5.23 lambs, of which 5.54 and 3.45 lambs were surviving to weaning. Our rates (2.93 lambs, 2.32 surviving to March) are derived from a small sample of ewes, involve lamb survival beyond weaning and incorporate a lower ewe lifespan than what Festa-Bianchet and Jorgenson (1996) report. The Yarrow-Castle reproductive rate during 2004 (0.32) was low since Singer et al. (2000) had comparable fecundity rates for declining bighorn populations (initial production of a lamb) of 0.36 for 4- to 8-year-olds and 0.29 for 9- to 14-year-olds. The numbers presented here representing the female lamb population are 50% of those reported by Singer et al. (2000). Singer et al. (2000) found increasing populations to have fecundity rates of 0.46 for 4- to 8-year-olds and 0.45 for 9- to 14-year-olds. These rates are similar to reproductive rates calculated to our area during 2003 (0.47) and 2005 (0.44). It is possible that the lower reproductive rate observed in 2004 (0.32) was a result of lambs dying before first visual confirmation, therefore any bias in reproduction would be toward a lower value. However, recruitment by radio-collared ewes in the Yarrow-Castle area (lamb surviving to 10 months) was low for all years, with an average of 0.18. Singer et al. (2000) found similar recruitment rates only in declining populations. Their declining populations exhibited recruitment rates of 0.12 for 4- to 8-year-olds and 0.17 for 9- to 14-year-olds, while their increasing populations had recruitment rates of 0.36 for 4- to 8-year-olds and 0.38 for 9- to 14-year-olds. Recruitment in the Yarrow-Castle population is consistent with rates observed in declining populations.

Population growth (λ)

Growth rate estimation for the Yarrow-Castle population incorporating a 2-age class (lamb and adult) matrix ranged from 1.018 to 1.064 with an average $\lambda = 1.047$, indicating the population is growing by approximately 5% per year. However, this level of growth was not observed in the aerial census trend data during the study period. It is possible that a 5% population increase may go undetected from one census to the next, depending on survey precision. Population growth may have been overestimated in the 2-age class matrix assuming 100% survival for yearlings. Since yearling survival in bovids is often lower and more variable than adult survival and higher and less variable than juvenile survival (in this case lamb survival; Gaillard et al. 2000), we estimated population growth using variations of yearling survival. Other studies have estimated yearling female bighorn survival ranging from 0.81 and 0.86 (Jorgenson et al. 1997, Loison et al. 1999), while some populations have experienced extreme yearling survival ranging from 0 to 100% (Jorgenson et al. 1997). Incorporating various yearling survival rates into a 3-age class matrix resulted in population growth that ranged from 0.930 to 1.041 among years with an average $\lambda = 0.994$. When utilizing an 87% yearling survival rate within the matrix, the average $\lambda = 1.025$ matched that of the increase observed during aerial census surveys between 2002 ($n = 158$) and 2005 ($n = 162$).

If we assume our estimates include the full range of variation, then the Yarrow-Castle bighorn population may occasionally be influenced by punctuated but sporadic predation events, and may be driven by density dependence and could be near their carrying capacity. Yarrow-Castle lamb survival and recruitment are low and population growth estimates are fluctuating around 1.0. Young are highly sensitive to limiting factors caused by population density or by stochastic environmental events (Gaillard et al. 1998). At high population densities, reproductive costs increase and lamb survival decreases (Festa-Bianchet and Jorgenson 1998, Festa-Bianchet et al. 1998, Portier et al. 1998, Bérubé et al. 1999, Coulson et al. 2000, Gallant et al. 2001).

One method to test if the Yarrow-Castle population is at carrying capacity would be to harvest a small number of bighorn ewes. If nursery herd densities were decreased at carrying capacity, lamb production and population growth should increase (Jorgenson et al. 1993*b*, Jorgenson et al. 1998, Wishart et al. 1996), increasing the overall health of the population. Nevertheless, if a rapid rate of increase was observed in the future, ewe harvests could be considered to reduce the risk of a pneumonia epizootic (Jorgenson et al. 1993*b*).

Bighorn ewe reproductive success decreases at increasing density because resources limit their fitness (Gallant et al. 2001). When resource conditions are optimal, bighorn sheep have the ability to double their population numbers in as little as three years (Wishart et al. 1996). Populations that exhibit slow growth rates, low productivity and low survival have likely exceeded their range capacity (Geist 1971). When habitat is limiting, lamb survival decreases, ewe survival decreases, and ram horn growth decreases (Demarchi et al. 2000, Festa-Bianchet 1988*b*, Festa-Bianchet and Jorgenson 1998, Portier et al. 1998, Festa-Bianchet et al. 2004). The habitat condition in the Yarrow-Castle area is largely unknown and requires further investigation. Increasing forage quantity and quality in the Yarrow-Castle area by using prescribed fire could improve overall population health. Fire suppression during the past century has dramatically changed the landscape and has likely altered the amount of range available to sheep. The last recorded wildfire (size unknown) in the Yarrow-Castle area was in 1936 (Alberta Sustainable Resource Development 2005). Prescribed burning increases herbaceous plants and removes obstructive shrubby plants; bighorn sheep select for these burned areas (Peek et al. 1979, McWhirter et al. 1992). Bighorn sheep populations benefit from newly formed food sources created by fire, avalanches, and mine reclamation (Wishart et al. 1996). There exists an opportunity to implement a habitat restoration strategy for the Yarrow-Castle bighorn sheep population. The restoration efforts could test whether fire suppression may have caused a long-term decline in suitable bighorn range, although this would require an adequate method of evaluating the effects of an applied burn and if it is in actuality improving forage quality for the Yarrow-Castle bighorn population.

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Literature cited

Alberta Environmental Protection. 1993. Management Plan for Bighorn Sheep in Alberta Wildlife Management, Ser. No. 6. Publ. T/248. Environmental Protection Fish and Wildlife Services, Edmonton, Alberta.

Alberta Sustainable Resource Development. 2005. Fire raging in Blind Canyon, taken from Cherry Hill (image 5581) [online]. Forest Protection Historical Image Library. Available from: http://www.srd.gov.ab.ca/wildfires/imagelibrary/[accessed 5 Dec 2007].

Bauer, J.W., K.A. Logan, L.L. Sweanor, and W.M. Boyce. 2005. Scavenging

Behavior in Puma. Southwest Naturalist 50: 466-471.

Bergerud, A.T., and J.P. Elliot. 1998. Wolf Predation in a Multi-ungulate System in Northern British Columbia. Canadian Journal of Zoology 76: 1551-1569.

Bérubé, C.H., M. Festa-Bianchet, and J.T. Jorgenson. 1999. Individual Differences, Longevity, and Reproductive Senescence in Bighorn Ewes. Ecology 80: 2555-2565.

Burles, D.W., and M. Hoefs. 1984. Winter Mortality of Dall sheep, *Ovis dalli*, in Kluane National Park, Yukon. Canadian Field Naturalist 98: 479-484.

Cassirer, E.F., and A.R.E. Sinclair. 2007. Dynamics of Pneumonia in a Bighorn Sheep Metapopulation. Journal of Wildlife Management 71: 1080-1088.

Caswell. H. 2001. Matrix Population Models: Construction, Analysis, and Interpretation. Sinauer, Sunderland, Mass.

Clark, J., and C. Bergman. 2005. Southern Bighorn Sheep Survey 2005 (WMU's 306, 308, 400 and 402). Sustainable Resource Development, Fish and Wildlife Division, Blairmore, Alberta.

Clover, M.R. 1954. A Portable Deer Trap and Catch-net. California Fish and Game Journal 40: 367-373.

Cougar Management Guidelines Working Group. 2005. Cougar Management Guidelines, first edition. WildFutures, Bainbridge Island, Wash.

Coulson, T., E.J. Milner-Gulland, and T. Clutton-Brock. 2000. The Relative Roles of Density and Climatic Variation on Population Dynamics and Fecundity Rates in Three Contrasting Ungulate Species. Proceedings of the Royal Society 267: 1771-1779.

Demarchi, R.A., C.L. Hartwig, and D.A. Demarchi. 2000. Status of California Bighorn Sheep in British Columbia. Ministry of Environment, Lands and Parks Wildlife Branch, Victoria, B.C.

Eccles, T.R., and D.M. Shackleton. 1979. Recent Records of Twinning in Mountain Sheep. Journal of Wildlife Management 43: 974-976.

Erickson, W.P., T.L. McDonald, K.G. Gerow, S. Howlin, and J.W. Kern. 2001. Statistical Issues in Resource Selection Studies with Radio-marked Animals. *In* Radio Tracking and Animal Populations. *Edited by* J.J. Millspaugh, and J.M. Marzluff. Academic Press, San Diego, Calif.

Festa-Bianchet, M. 1987. Bighorn Sheep, Climbing Accidents, and Implications for Mating Strategy. Mammalia 51: 618-620.

Festa-Bianchet, M. 1988*a*. Seasonal Range Selection in Bighorn Sheep: Conflicts between Forage Quality, Forage Quantity, and Predator Avoidance. Oecologia 75: 580-586.

Festa-Bianchet, M. 1988*b*. Birthdate and Survival in Bighorn Lambs (*Ovis canadensis*). Journal of Zoology (*London)* 214: 653-661.

Festa-Bianchet, M. 1988*c*. Age-specific Reproduction of Bighorn Ewes in Alberta, Canada. Journal of Mammalogy 69: 157-160.

Festa-Bianchet, M. 1988*d*. Nursing Behaviour of Bighorn Sheep: Correlates of Ewe Age, Parasitism, Lamb Age, Birthdate and Sex. Animal Behaviour 36: 1445-1454.

Festa-Bianchet, M. 1992. Use of Age Ratios to Predict Bighorn Sheep Population Dynamics. *In* Proceedings of Eighth Biennial Wild Sheep and Goat Council Conference, Cody, Wyoming, Apr. 27-May 1, 1992. Northern Wild Sheep and Goat Council. pp. 227-236.

Festa-Bianchet, M., and J.T. Jorgenson. 1996. Variability in Lifetime Reproductive Success of Bighorn Ewes. *In* Proceedings of Tenth Biennial Wild Sheep and Goat Council Conference, Silverthorne, Colorado, Apr. 30-May 3, 1996. Northern Wild Sheep and Goat Council. pp. 7-10.

Festa-Bianchet, M., and J.T. Jorgenson. 1998. Selfish Mothers: Reproductive Expenditure and Resource Availability in Bighorn Ewes. Behavioural Ecology 9: 144-150.

Festa-Bianchet, M., J.T. Jorgenson, and W.D. Wishart. 1994. Early Weaning in Bighorn Sheep, *Ovis canadensis*, Affects Growth of Males but not Females. Behavioural Ecology 5: 21-27.

Festa-Bianchet, M., J.T. Jorgenson, M. Lucherini, and W.D. Wishart. 1995. Life History Consequences of Variation in Age of Primiparity in Bighorn Ewes. Ecology 76: 871-881.

Festa-Bianchet, M., J-M. Gaillard, and J.T. Jorgenson. 1998. Mass and Density Dependent Reproductive Success and Reproductive Costs in a Capital Breeder. American Naturalist 152: 367-379.

Festa-Bianchet, M., D.W. Coltman, L. Turelli, and J.T. Jorgenson. 2004. Relative Allocation to Horn and Body Growth in Bighorn Rams Varies with Resource Availability. Behavioural Ecology 15: 305-312.

Festa-Bianchet, M., T. Coulson, J-M. Gaillard, J.T. Hogg, and F. Pelletier. 2006. Stochastic Predation Events and Population Persistence in Bighorn Sheep. Proceedings of the Royal Society of London 273: 1537-1543.

Gaillard, J-M., M. Festa-Bianchet, N.G. Yoccoz. 1998. Population Dynamics of Large Herbivores: Variable Recruitment with Constant Adult Survival. Tree 13: 58-63.

Gaillard, J-M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal Variation in Fitness Components and Population Dynamics of Large Herbivores. Annual Review of Ecology and Systematics 31:367-393.

Gallant, B.Y., D. Réale, and M. Festa-Bianchet. 2001. Does Mass Change of Primiparous Bighorn Ewes Reflect Reproductive Effort?. Canadian Journal of Zoology 79: 312-318.

Garshelis, D.L., M.L. Gibeau, and S. Herrero. 2005. Grizzly Bear Demographics in and around Banff National Park and Kananaskis Country, Alberta. Journal of Wildlife Management 69: 277-297.

Geist, V. 1966. Validity of Horn Segment Counts in Aging Bighorn Sheep. Journal of Wildlife Management 30: 634-646.

Geist, V. 1971. Mountain Sheep: a Study in Behavior and Evolution. University of Chicago Press, Chicago, Illinois.

Geist, V. 1975. On the Management of Mountain Sheep: Theoretical Considerations. *In* The Wild Sheep of North America. *Edited by* J.B. Trefethen. Boone and Crockett Club, Alexandria, Virginia.

Girard, I., J. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of Sampling Effort Based on GPS Telemetry on Home-range Size Estimations. Journal of Wildlife Management 66: 1290-1300.

Goodson, N.J., D.R. Stevens, and J.A. Bailey. 1991. Winter-spring Foraging Ecology and Nutrition of Bighorn Sheep on Montane Ranges. Journal of Wildlife Management 55: 422-433.

Gonzalez-Voyer, A., M. Festa-Bianchet, and K.G. Smith. 2001. Efficiency of Aerial Surveys of Mountain Goats. Wildlife Society Bulletin 29: 140-144.

Green, G.I., D.J. Mattson, and J.M. Peek. 1997. Spring Feeding on Ungulate Carcasses by Grizzly Bears in Yellowstone National Park. Journal of Wildlife Management 61:1040-1055.

Hamel, S., S.D. Côté, K.D. Smith, and M. Festa-Bianchet. 2006. Population Dynamics and Harvest Potential of Mountain Goat Herds in Alberta. Journal of Wildlife Management 70: 1044-1053.

Hayes, C.L., E.S. Rubin, M.C. Jorgensen, R.A. Botta, and W.M. Boyce. 2000. Mountain Lion Predation of Bighorn Sheep in the Peninsular Ranges, California. Journal of Wildlife Management 64: 954-959.

Hood, G.M. 2006. PopTools extension version 2.7.5. [online]. Available from: http://www.cse.csiro.au/poptools [accessed Jan 2007].

Hornocker, M.G., and H.S. Hash. 1981. Ecology of the Wolverine in Northwestern Montana. Canadian Journal of Zoology 59: 1286-1301.

Jacobson, A.R., A. Provenzale, A.von Hardenberg, B. Bassano, and M. Festa-Bianchet. 2004. Climate Forcing and Density Dependence in a Mountain Ungulate Population. Ecology 85:1598-1610.

Jorgenson, J.T., M. Festa-Bianchet, and W.D. Wishart. 1993*a*. Effects of Body Size, Population Density, and Maternal Characteristics on Age at First Reproduction in Bighorn Ewes. Canadian Journal of Zoology 71: 2509-2517.

Jorgenson, J.T., M. Festa-Bianchet, and W.D. Wishart. 1993*b*. Harvesting Bighorn Ewes: Consequences for Population Size and Trophy Ram Production. Journal of Wildlife Management 57: 429-435.

Jorgenson, J.T., M. Festa-Bianchet, J-M. Gaillard and W.D. Wishart. 1997. Effects of Age, Sex, Disease, and Density on Survival of Bighorn Sheep. Ecology 78: 1019-1032.

Jorgenson, J.T., M. Festa-Bianchet, and W.D. Wishart. 1998. Effects of Population Density on Horn Development in Bighorn Rams. Journal of Wildlife Management 62: 1011-1020.

Kamler, J.F., R.M. Lee, J.C. deVos Jr., W.B. Ballard, and H.A. Whitlaw. 2003. Mortalities from Climbing Accidents of Translocated Bighorn Sheep in Arizona. Southwest Naturalist 48: 145-147.

Kenney, A.J., and C.J. Krebs. 2003. Ecological Methodology Version 6.1.1. [computer program]. Dept. Zool., Univ. B.C., Vancouver, B.C.

Krebs, C.J. 1999. Ecological Methodology. Addison-Wesley Educational Publishers, Inc., Menlo Park, Calif.

Landa, A., O. Strand, J.E. Swenson, and T. Skogland. 1997. Wolverines and Their Prey in Southern Norway. Canadian Journal of Zoology 75: 1292-1299.

Leslie, P.H. 1945. On the Use of Matrices in Certain Population Mathematics. Biometrika 33: 183-212.

Loison, A., M. Festa-Bianchet, J-M. Gaillard, J.T. Jorgenson, and J-M. Jullien. 1999. Age Specific Survival in Five Populations of Ungulates: Evidence of Senescence. Ecology 80: 2539-2554.

MacCallum, B.N., and V. Geist. 1992. Mountain Restoration: Soil and Surface Wildlife Habitat. GeoJournal 27: 23-46.

Mattson, D.J. 1997. Use of Ungulates by Yellowstone Grizzly Bears *Ursus arctos*. Biological Conservation 81: 161-177.

McLoughlin, P.D., E. Dzus, B. Wynes, and S. Boutin. 2003. Declines in Populations of Woodland Caribou. Journal of Wildlife Management 67: 755-761.

McWhirter, D., S. Smith, E. Merrill, and L. Irwin. 1992. Foraging Behavior and Vegetation Responses to Prescribed Burning on Bighorn Sheep Winter Range. *In* Proceedings of Eighth Biennial Wild Sheep and Goat Council Conference, Cody, Wyoming, Apr. 27-May 1, 1992. Northern Wild Sheep and Goat Council. pp.264-278.

Murphy, E.C., F.J. Singer, and L. Nichols. 1990. Effects of Hunting on Survival and Productivity of Dall Sheep. Journal of Wildlife Management 54: 284-290.

Onderka, D.K., and W.D. Wishart.1984. A Major Bighorn Sheep Die-off from Pneumonia in Southern Alberta. *In* Proceedings of Fourth Biennial Wild Sheep and Goat Council Conference, Whitehorse, Yukon, Apr. 30-May 3, 1984. Northern Wild Sheep and Goat Council. pp.356-363.

Peek, J.M., R.A. Riggs, and J.L. Lauer. 1979. Evaluation of Fall Burning on Bighorn Sheep Winter Range. Journal of Range Management 32: 430-432.

Pollock, K.H., S.R. Winterstein, C.M Bunck, and P.D. Curtis. 1989. Survival Analysis in Telemetry studies: The Staggered Entry Design. Journal of Wildlife Management 53: 7-15.

Portier, C., M. Festa-Bianchet, J-M. Gaillard, J.T. Jorgenson, and N.G. Yoccoz. 1998. Effects of Density and Weather on Survival of Bighorn Sheep Lambs (*Ovis canadensis*). Journal of Zoology (*London*) 245: 271-278.

Réale, D., and M. Festa-Bianchet. 2003. Predator-induced Natural Selection on Temperament in Bighorn Ewes. Animal Behaviour 65: 463-470.

Risenhoover, K.L., J.A. Bailey, and L.A. Wakelyn. 1988. Assessing the Rocky Mountain Bighorn Sheep Management Problem. Wildlife Society Bulletin 16: 346-352.

Rodgers, A.R., and A.P. Carr. 1998. HRE: The Home Range Extension for ArcView. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ont.

Ross, P.I., M.G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar Predation on Bighorn Sheep in Southwestern Alberta during Winter. Canadian Journal of Zoology 75: 771-775.

Seip, D.R., and F.L. Bunnell. 1985. Foraging Behavior and Food Habits of Stone’s Sheep. Canadian Journal of Zoology 63: 1638-1646.

Singer, F.J., E. Williams, M.W. Miller, and L.C. Zeigenfuss. 2000. Population Growth, Fecundity, and Survivorship in Recovering Populations of Bighorn Sheep. Restoration Ecology 8: 75-84.

Stelfox, J.G. 1976. Range Ecology of Rocky Mountain Bighorn Sheep. Canadian Wildlife Service Report Series No. 39. Edmonton, Alberta.

Tsai, K., K.H. Pollock, and C. Brownie. 1999. Effects of Violation of Assumptions for Survival Analysis Methods in Radiotelemetry Studies. Journal of Wildlife Management 63: 1369-1375.

van Zyll de Jong, C.G. 1975. The Distribution and Abundance of the Wolverine *(Gulo gulo)* in Canada. Canadian Field Naturalist 89: 431-437.

Wishart, W., B. MacCallum, and J.T. Jorgenson. 1996. Lessons Learned from Rates of Increase in Bighorn Herds. Alberta Department of Environmental Protection, Edmonton, Alberta.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, N.J.

List of tables and appendices

Table 1. Kaplan-Meier 3-year cumulative survival estimates for bighorn ewes in the Yarrow-Castle study area, Alberta based on annual survival, core residence, seasonal period, and mortality type, 2003-2005.

Year	Number of ewes	Number of mortalities	Annual survival rate (95% CI)	SE
2003	29	5	0.83 (0.70 - 0.97)	0.07
2004	30	3	0.90 (0.79 - 1.00)	0.06
2005	27	3	0.89 (0.77 - 1.00)	0.06
Core area	**Number of ewes**	**Number of mortalities**	**Cumulative survival rate (95% CI)**	**SE**
Southern	15	7	0.48 (0.22 - 0.75)	0.13
Central	8	2	0.75 (0.45 - 1.00)	0.15
Northern	7	2	0.73 (0.42 - 1.00)	0.16
Seasonal period	**Number of ewes**	**Number of mortalities**	**Cumulative survival rate (95% CI)**	**SE**
Winter	31	5	0.84 (0.71 - 0.97)	0.07
Summer	29	5	0.82 (0.68 - 0.96)	0.07
Fall	25	1	0.96 (0.90 - 1.00)	0.04
Mortality type	**Number of ewes**	**Number of mortalities**	**Cumulative survival rate (95% CI)**	**SE**
Predator	35	7	0.77 (0.62 - 0.92)	0.08
Non-predator	35	4	0.86 (0.74 - 0.99)	0.06

Table 2. Survival (to approximately 10 months of age) of bighorn lambs born to radio-collared ewes in the Yarrow-Castle study area, Alberta, 2003-2005.

Year	Marked Ewes		Lambs			
	Total (*n*)	Total lambed	Total (*n*)	Mortalities	Survival (95% CI)	SE
2003	29	27 (93%)	27	16	0.41 (0.38-0.43)	0.01
2004	37	24 (65%)	24	11	0.54 (0.51-0.57)	0.02
2005	25	22 (88%)	22	13	0.41 (0.38-0.44)	0.01

Table 3. Variants of population growth (λ) for the Yarrow-Castle bighorn population, Alberta, 2003-2005.

Matrix stage	2003	2004	2005	Average
2-age class (100% yrlg. surv.)	1.018	1.064	1.060	1.047
3-age class (87% yrlg. surv.)	0.997	1.041	1.036	1.025
3-age class (66% yrlg. surv.)	0.965	1.013	1.007	0.995
3-age class (45% yrlg. surv.)	0.930	0.982	0.975	0.962

Appendix A. Bighorn ewe inter-birth intervals in the Yarrow-Castle study area, Alberta, 2003-2005.

Ewe I.D.	Year				Interbirth interval	
	2003	2004	2005		Lamb produced	Lamb surviving
0.003	1	1	1		1	1
0.009	1	0	0		2	
0.015	0	0	0		2	
0.021	0	0	1		1	
0.030	1	0	0		2	
0.040	1	0	1		1	2
0.058	0	1	0		1	
0.071	1	1	0			
0.090	0	0	0			
0.105	0					
0.145	1	0	0		2	
0.170	0	0	0		1	
0.201	0	0				
0.266	0	1	0			
0.308	0	0			1	
0.356	1	1	0		1	
0.508	0	1	0		1	
0.528	0					
0.534	1					
0.590	1	0	1		1	2
0.717	1	0	1		2	2
0.761	1	0	1		2	2
0.995	0	0	0		2	
1.183	0	0			1	
1.814	0	1	1		1	
1.830	0	0	0		2	
0.355	0					
0.080	0	0			1	
0.380	0	1			1	
0.328_04		0	0		1	
0.735_04		1	0		1	
0.650_04		1	1		1	1
0.105_04		0	1		1	
0.160		1				
0.340		0				
0.300		0				
0.420		1				
0.240		0	0			
0.100a		0				
0.500		1				
0.130		0				
		Average interval			1.32	1.67

0	No reproduction observed
0 (shaded)	Produced lamb but lamb did not survive to 10 months of age
1	Produced lamb and lamb survived to 10 months of age

Appendix B. Bighorn ewe reproductive rates in the Yarrow-Castle study area, Alberta, 2003-2005.

Ewe I.D.	Year			Lambs	Female lambs	Years observed	Reproduction rate
	2003	2004	2005				
0.003	1	1	1	3	1.5	3	0.50
0.009	1	0	1	2	1.0	3	0.33
0.015	1	0	1	2	1.0	3	0.33
0.021	1	1	1	3	1.5	3	0.50
0.030	1	0	1	2	1.0	3	0.33
0.040	1	1	1	3	1.5	3	0.50
0.058	1	1	1	3	1.5	3	0.50
0.071	1	1	0	2	1.0	3	0.33
0.090	0	1	1	2	1.0	3	0.33
0.105	1			1	0.5	1	0.50
0.145	1	0	1	2	1.0	3	0.33
0.170	1	1	1	3	1.5	3	0.50
0.201	0	0		0	0.0	2	
0.266	1	1	0	2	1.0	3	0.33
0.308	1	1		2	1.0	2	0.50
0.356	1	1	1	3	1.5	3	0.50
0.508	1	1	1	3	1.5	3	0.50
0.528	1			1	0.5	1	0.50
0.534	1			1	0.5	1	0.50
0.590	1	1	1	3	1.5	3	0.50
0.717	1	0	1	2	1.0	3	0.33
0.761	1	0	1	2	1.0	3	0.33
0.995	1	0	1	2	1.0	3	0.33
1.183	1	1		2	1.0	2	0.50
1.814	1	1	1	3	1.5	3	0.50
1.830	1	0	1	2	1.0	3	0.33
0.355	1			1	0.5	1	0.50
0.080	1	1		2	1.0	2	0.50
0.380	1	1		2	1.0	2	0.50
0.328_04		1	1	2	1.0	2	0.50
0.735_04		1	1	2	1.0	2	0.50
0.650_04		1	1	2	1.0	2	0.50
0.105_04		1	1	2	1.0	2	0.50
0.160		1		1	0.5	1	0.50
0.340		1		1	0.5	1	0.50
0.300		0		0	0.0	1	
0.420		1		1	0.5	1	0.50
0.240		0	0	0	0.0	2	
0.100a		0		0	0.0	1	
0.500		1		1	0.5	1	0.50
0.130		0		0	0.0	1	
Female lambs	13.5	12.0	11.0		36.5		
Adult females	29	37	25		Sum	91	
Annual repro. rate	0.47	0.32	0.44			Sum	0.40
							Overall

0	No reproduction observed
1	Produced lamb but lamb did not survive to 10 months of age
1	Produced lamb and lamb survived to 10 months of age

Appendix C. Bighorn ewe recruitment rates in the Yarrow-Castle study area, Alberta, 2003-2005.

Ewe I.D.	Year			Lambs	Female lambs	Years observed	Recruitment rate
	2003	2004	2005				
0.003	1	1	1	3	1.5	3	0.50
0.009	1	0	0	1	0.5	3	0.17
0.015	0	0	0	0	0.0	3	0.00
0.021	0	0	1	1	0.5	3	0.17
0.030	1	0	0	1	0.5	3	0.17
0.040	1	0	1	2	1.0	3	0.33
0.058	0	1	0	1	0.5	3	0.17
0.071	1	1	0	2	1.0	3	0.33
0.090	0	0	0	0	0.0	3	0.00
0.105	0			0	0.0	1	0.00
0.145	1	0	0	1	0.5	3	0.17
0.170	0	0	0	0	0.0	3	0.00
0.201	0	0		0	0.0	2	
0.266	0	1	0	1	0.5	3	0.17
0.308	0	0		0	0.0	2	0.00
0.356	1	1	0	2	1.0	3	0.33
0.508	0	1	0	1	0.5	3	0.17
0.528	0			0	0.0	1	0.00
0.534	1			1	0.5	1	0.50
0.590	1	0	1	2	1.0	3	0.33
0.717	1	0	1	2	1.0	3	0.33
0.761	1	0	1	2	1.0	3	0.33
0.995	0	0	0	0	0.0	3	0.00
1.183	0	0		0	0.0	2	0.00
1.814	0	1	1	2	1.0	3	0.33
1.830	0	0	0	0	0.0	3	0.00
0.355	0			0	0.0	1	0.00
0.080	0	0		0	0.0	2	0.00
0.380	0	1		1	0.5	2	0.25
0.328_04		0	0	0	0.0	2	0.00
0.735_04		1	0	1	0.5	2	0.25
0.650_04		1	1	2	1.0	2	0.50
0.105_04		0	1	1	0.5	2	0.25
0.160		1		1	0.5	1	0.50
0.340		0		0	0.0	1	0.00
0.300		0		0	0.0	1	
0.420		1		1	0.5	1	0.50
0.240		0	0	0	0.0	2	
0.100a		0		0	0.0	1	
0.500		1		1	0.5	1	0.50
0.130		0		0	0.0	1	
Female lambs	5.5	6.5	4.5		16.5		
Adult females	29	37	25		Sum	91	
Annual recruit. rate	0.19	0.18	0.18			Sum	0.18
							Overall

0	No reproduction observed
0	Produced lamb but lamb did not survive to 10 months of age
1	Produced lamb and lamb survived to 10 months of age