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Table of Contents

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IDENTIFICATION OF BIGHORN SHEEP MIGRATION CORRIDORS USING GPS TELEMETRY SYSTEMS

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Abstract: Employing Global Positioning System (GPS) telemetry collars, an ongoing 3-year study of the Fraser River/Marble Range California bighorn sheep population is 1) evaluating the utility of a GPS animal location system in defining the movement corridors of large ungulates, and 2) identifying migration routes of the local sheep herd and determining migration timing between seasonal ranges. The importance of historically known summer habitats in the Marble Range mountains has been confirmed, and 2 distinct migration routes have been defined, based on satellite location fixes collected on 15-minute intervals. Preliminary data suggest that, once initiated, animals navigate migration corridors without delay, as indicated by rates of travel recorded for an adult ram (0 = 2.64 ± 0.18 km/hour) and an adult ewe (0 = 1.60 ± 0.09 km/hour).

Development in the Marble Range region of the southern interior of British Columbia may negatively impact the integrity of important summer range and migration corridors of the local bighorn population. Continuing work is expanding knowledge of seasonal habitat use patterns in the area and identifying additional migration routes. This information will ultimately be incorporated into land use guidelines sensitive to the requirements of the local bighorn population.

Key words: bighorn sheep, *Ovis canadensis californiana*, migration corridors, British Columbia, global positioning system.

The Fraser River (East) California bighorn sheep (*Ovis canadensis californiana*) population of the southern interior of British Columbia is comprised of both migratory and non-migratory sub-populations. Non-migratory animals spend the majority of their lives within sight of the Fraser River. Migratory individuals, by contrast, travel seasonally between low elevation slopes and benches on the eastern bank of the Fraser River, and high elevation alpine meadow habitats in the Marble Range mountains to the east. Historically, the migratory sub-population, comprising up to 50% of the herd, moved between the Fraser River and the Marble Range in many locations; however, over the past 4 decades, the northern migration routes have been abandoned, and the southern corridors now exclusively support seasonal movements (D. Eyer, Clinton and District Outdoor Sportsmen Association, personal communication). Evidence suggests that 25% of the herd currently exhibits migratory behaviour. Several factors have been implicated in the shift to the southern routes, including rural residential development, power line construction, timber harvesting activities and the loss of older sheep that used these routes. The result has been an increasing number of sheep remaining on the Fraser River winter range year-round. The higher density of animals on this range has degraded forage quality, and has been implicated in a recent lungworm-induced pneumonia die-off (B.C. Environment, unpublished data). A significant reduction in lamb recruitment resulted in an increasing population of approximately 400 animals being reduced by 40-50% over a 3-year period (1990-1993). Annual aerial surveys throughout the mid-1990s indicated that lamb recruitment was still at low levels (B.C. Environment, unpublished data). A recovery in lamb recruitment was evident beginning in 1997, although population levels are not responding yet.

Preserving the remaining southern migration routes will permit migratory individuals to take advantage of high quality summer forage in alpine areas and, subsequently, may reduce the likelihood of future die-off events by decreasing population densities on over-exploited low elevation habitats. Two provincial parks, Marble Range and Edge Hills, have recently been established in the region, protecting valuable sheep habitat. However, important summer range and portions of the suspected southern migratory corridors lie within an area held in mining claims, which were excluded from the parks. Timber harvesting and the installation of an electrical transmission line have altered the landscape in the valley situated between the Marble Range and the Edge Hills, although the impact of these changes on the migratory behaviour of this herd is presently unknown. Risenhoover and Bailey (1985) reported that mountain sheep avoided dense, tall vegetation, such as Douglas fir stands; preferred habitats included open areas where acceptable forage densities and visibility (i.e. predator detection) were greater. Radio telemetry work on the Churn Creek herd of British Columbia also suggested that animals were travelling quickly along the forested portions of an identified migration route (Keystone Wildlife Research 1998).

This study was developed to 1) evaluate the utility of Global Positioning System (GPS) telemetry systems in defining movement corridors for large ungulates and 2) identify and accurately map the remaining bighorn sheep migration corridors in the Fraser River/Marble Range area. The project was initiated in 1998, and is scheduled to continue through mid-2001.

STUDY AREA

The study area encompasses approximately 500 km^2 east of the Fraser River, 200 km northeast of the city of Vancouver, B.C. Elevations range from approximately 250 m on the Fraser River in the west to 2250 m in the Marble Range mountains to the east (Fig. 1).

High elevation alpine meadows, where sedges (*Carex* spp.), grasses and forbs predominate, and scattered stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), are representative of bighorn sheep summer habitat in the Marble Range mountains. The western margin of the range drops precipitously through limestone cliffs to the Kostering Creek valley. The area experiences cool short growing seasons, while winters are long and cold. Mean annual precipitation is 400-500 mm, most of which (50-70%) falls as snow (Meidinger and Pojar 1991). Sheep winter range on the Fraser River includes the western slopes of the Edge Hills, where open stands of Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) predominate. The sagebrush (*Artemisia tridentata*)/bunchgrass (*Elymus spicatus*) benches above the Fraser River (450 m in elevation) are also utilized. This area is characterized by hot, dry summers, with substantial growing season moisture deficits common. Winters are cool and 20-50% of mean annual precipitation (300 mm) falls as snow.

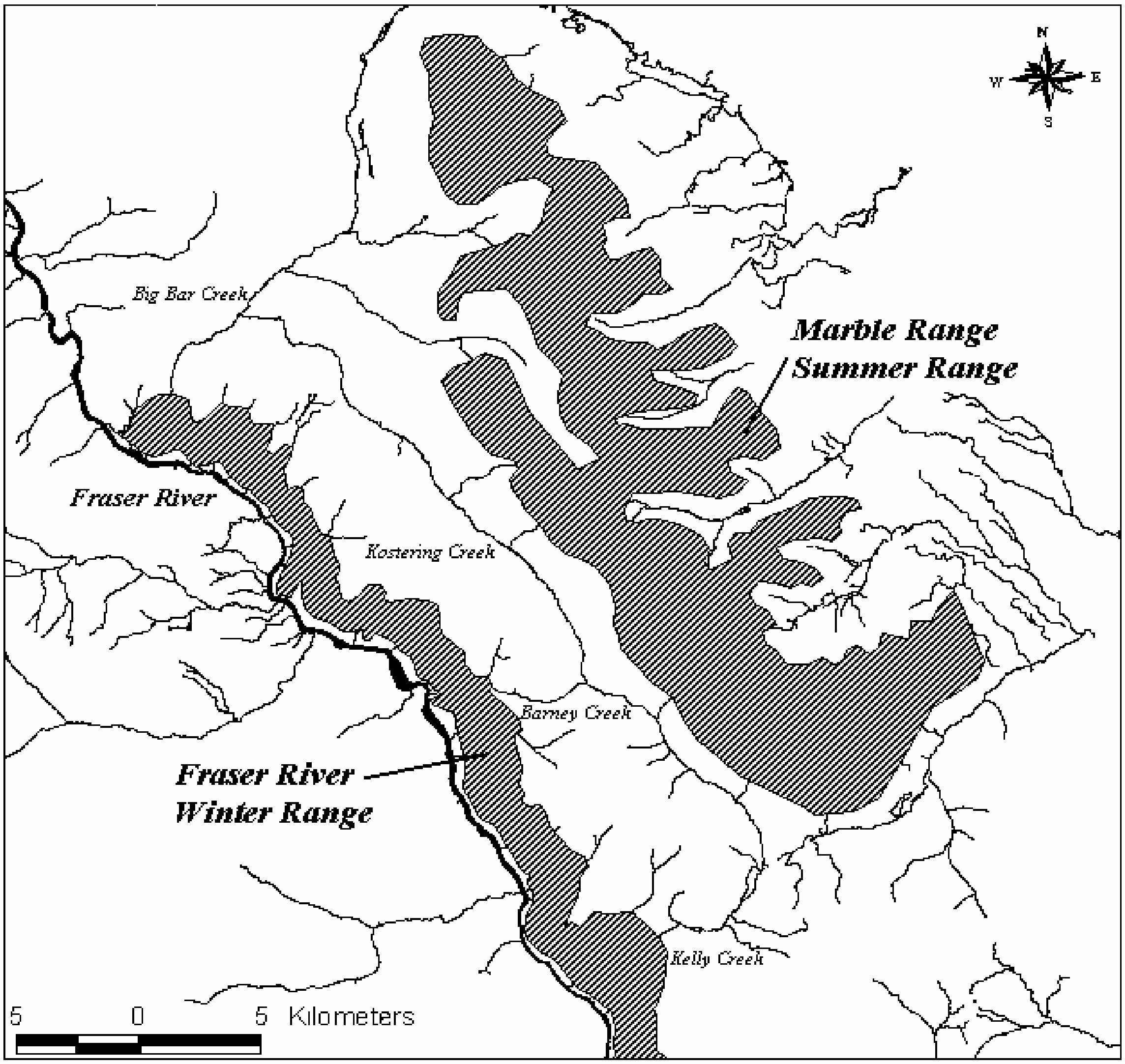

Fig. 1. Marble Range bighorn sheep seasonal ranges

METHODS

Animal Capture and Collaring

Animals were captured in late summer, prior to expected migration from summer to winter range. Sheep were captured via helicopter netgunning using a Bell 206B JetRanger. On the ground, sheep were blindfolded and hobbled. Once the animal was restrained, an Advanced Telemetry Systems (ATS, Isanti, Minnesota) Global Positioning System (GPS) collar, equipped with a VHF transmitter and a remotely activated release mechanism, was readied for deployment. The units weighed 950 g, and were programmed to fix their location every 15 minutes. Battery life was calculated at 40-50 days at this fix interval. The collar's GPS receiver was initialized according to manufacturer's instructions (ATS 1998), during which time the animal's neck measurement was taken, age was determined (based on horn annuli), and an assessment of general health was completed. Upon successful completion of the initialization sequence, the collar was placed on the animal, the hobbles and blindfold removed, and the animal released. Collar functioning was reconfirmed using a Telonics TR-2 telemetry receiver. Lotek LMRT-3 VHF telemetry collars (Lotek Engineering, Newmarket, Ontario) were available, to be used in cases of multiple-animal captures.

Two animals, a 4-year-old ram (Ram #128-1) and a 5-year-old ewe (Ewe #129), were captured on summer range and fitted with GPS collars on 19 August 1999. A second ram captured with the first received a VHF collar. The GPS collar was carried by the ram for 20 days before the unit was released on 7 September 1999, to confirm collar functioning. The collar on the ewe was released after 39 days (26 September 1999).

A 7-year-old ram (Ram #128-2) was captured on the Marble Range summer habitat and fitted with a GPS collar on 2 November 1999. The unit remained on the animal for 38 days, before being released on 9 December 1999.

Monitoring and Collar Retrieval

Approximately 40 days after collar deployment, a monitoring flight was undertaken, and the location of the collared animal(s) determined. If the animal had traveled between its seasonal ranges, the ATS triggering transmitter unit was employed to activate the release mechanism on the collar. Once released from the animal, the collar was located and retrieved.

Data Analyses

Offloading of data from the collar GPS receivers was accomplished using a PC-based system running ATS Collar (Version 13) software. The data collected and stored in the collars' on-board memory included the date, time, horizontal position, elevation, fix type [2- or 3-dimensional (2D or 3D)], satellite information, positional dilution of precision (PDOP) and the time required to obtain a fix during each specified interval. Data required for differential correction were not collected in the current ATS collar model.

Location data were imported into ArcView GIS Version 3.0a (Environmental Systems Research Institute, Redlands, California) for plotting and analyses. All calculated distances are linear.

RESULTS

Movements and Migration Corridors

The GPS collar carried by Ram #128-1 recorded 862 fixes; due to an oversight in collar programming, this unit collected locations once every 30 minutes. Eighty-one percent of fixes were 3D. The mean PDOP value for locations was 3.56. This animal remained on summer range throughout the collar trial. He moved about near the capture site for 0.5 days, and then moved approximately 9 km south, where he remained for another 0.5 days. He then traveled an additional 6 km towards the southern end of the Marble Range, where he remained until the collar was released (Fig. 2). Major movements were initiated during the early morning hours (0530 – 0700 hrs) and completed by mid-afternoon (1600 hrs).

The second collar (Ewe #129) collected 3,154 location fixes, with 82% recorded as 3D. The mean PDOP was 3.68. This animal moved from the Marble Range to the Fraser River winter range on 3 September, and then traveled back to summer habitat on 16 September, where she remained until the collar was released on 26 September. The collar's GPS receiver did not record the animal's locations on the route from the mountains to the Fraser River; however, the return trip in mid-September was successfully fixed (Fig. 3). This corridor covered a distance of approximately 8 km, which the animal traveled in 4 hours and 45 minutes between 1214 and 1700 hrs. Once initiated, movement between seasonal ranges progressed steadily, at a mean rate of travel of 1.60 ± 0.09 km/hour. The collar on Ram #128-2 recorded 3,070 locations, 82% of which were 3D. Mean PDOP was 3.43. The animal's migration movement from the Marble Range to the Fraser River occurred on 10 November during the early afternoon hours (1248 – 1603 hrs; 3 hrs 14 min) and covered approximately 8 km (Fig. 4). Mean movement rate through the corridor was 2.46 ± 0.18 km/hour.

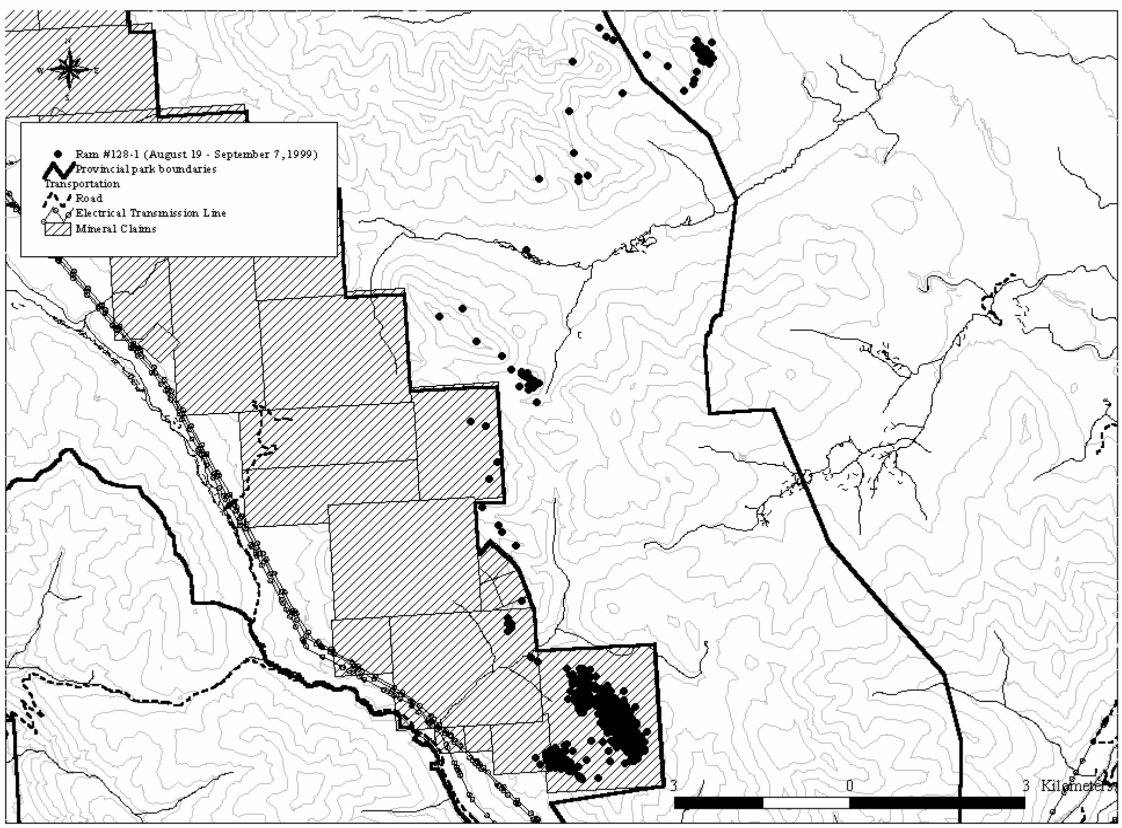

Fig. 2. GPS location data for Ram #128-1: 19 August September 1999

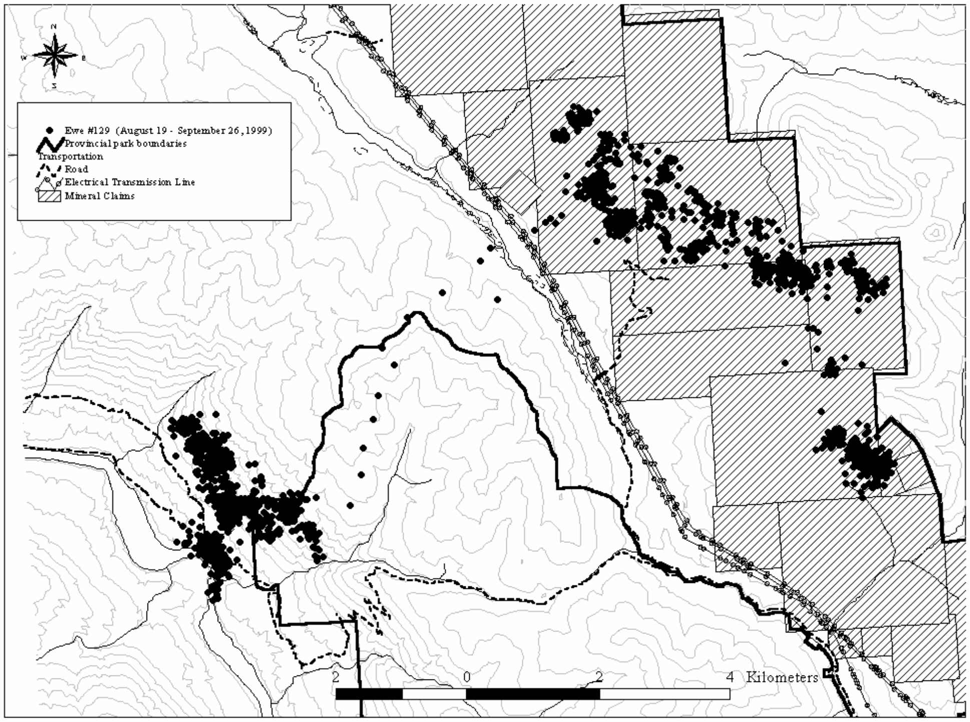

Fig. 3. GPS location data for Ewe #129: 19 August – 26 September 1999

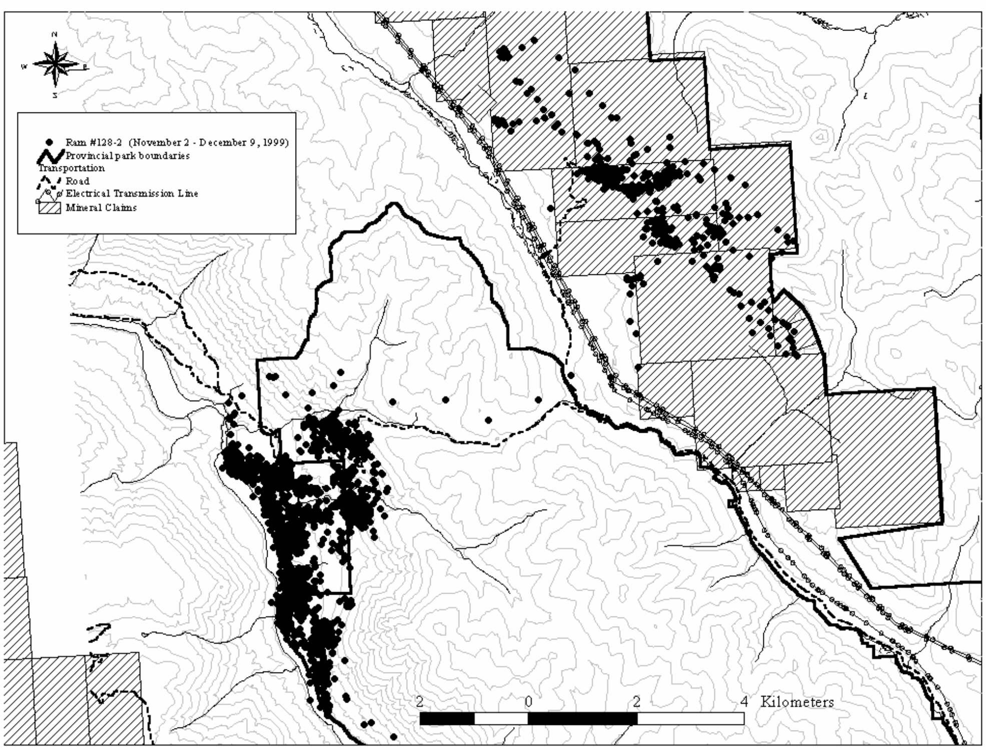

Fig. 4. GPS location data for Ram #128-2: 2 November – 9 December 1999

DISCUSSION

GPS Utility

Preliminary data from GPS-collared bighorn sheep of the Fraser River/Marble Range herd indicate that GPS telemetry systems can be an extremely valuable tool in identifying important movement and migration routes for large ungulates. The advantages of GPS collars versus VHF units in wildlife research are many, and generally outweigh the higher cost, variable reliability and increased complexity of data handling required (Kinley 1998). For the purposes of the current project, where the focus was a well-defined time window (i.e. migration), the ability to program these units for short intervals between fix attempts (i.e. every 15 minutes), maximizes data collected, ultimately providing a precise definition of travel routes. GPS systems are also more likely to record use of special habitat features, such as mineral licks, which are visited infrequently. VHF telemetry monitoring is restricted to daylight hours and conditions optimal for flying, whereas GPS systems are less biased with respect to time of day and weather conditions. GPS collar data, however, may be more biased relative to habitat type and topography than is VHF data, because of signal transmission interference (Rempel et al. 1995, Moen et al. 1996). The disturbance associated with aerial telemetry monitoring, which may result in animals altering their movements and habitat selection patterns (Poole and Heard 1998), is eliminated with the use of data retention GPS collars.

The high percentage of 3D versus 2D fixes obtained in this study is significant compared to other recent studies utilizing GPS collars on mountain ungulates. Poole (1998) reported 30% and 67% 3D fixes, respectively, using 2 ATS prototype collars on mountain goats in east-central British Columbia. An ongoing mountain caribou study being conducted in the Wells Gray region of B.C. reported 38% 3D fixes (Norquay 1999). Fix accuracy is improved considerably when a 3D fix (i.e. 4 or more satellites available) is obtained (Moen et al. 1997, Rempel and Rodgers 1997). Indeed, Norquay (1999) suggested that all non-differentially corrected 2D fixes and differentially corrected 2D fixes with PDOP values greater than 4.5 should be rejected, as much of the error associated with these data (resulting from poor satellite geometry) are larger and more difficult to assess than that for 3D data. Based on a review of recent literature, a mean error of 60-80 m (95% within 250 m) may be expected with 2D non-differentially corrected fixes (Timberland Consultants, unpublished data). The collars used in the current study did not permit differential correction of satellite locations; however, the comparatively small percentage of 2D fixes, low mean PDOP values associated with these fixes (3.47), and the level of precision deemed necessary to evaluate seasonal habitat use and delineate migration corridors, i.e. 300-500 m width proposed, justified retaining all location points for plotting. The recent removal of selective availability error from GPS receivers (1 May 2000) has rendered differential correction processes obsolete. Units deployed subsequent to this date are expected to obtain location fixes accurate to within 10 m.

Technical Difficulties

Several technical difficulties were encountered during these initial stages of the project, all of which were diagnosed and corrected. The first remote release of a GPS collar in September was accomplished without difficulty; however, immediately afterwards, attempts to release the second collar failed. An electronic malfunction associated with the triggering transmitter's power source was diagnosed and repaired by ATS. Subsequent release operations were accomplished without incident.

The failure of the ewe's GPS unit to record locations through a 2.5-hour time block during her movement between the Marble Range and the Fraser River on 3 September 1999 is inexplicable. Data sets exhibit gaps of 30-45 minutes, where an insufficient number of satellites were available to obtain a fix; however, gaps of 1 hour were infrequent and greater than 1 hour, rare. Vegetation (i.e. canopy cover) and topographic relief both affect satellite acquisition through signal interference. Although receiver malfunction cannot be ruled out, the incidence of data gaps of varying duration indicate that features of the habitat are the most likely explanation for the incomplete location data.

Seasonal Range and Migration Corridors

Data available to date suggest that the rugged southwestern extent of the Marble Range, west of the Marble Range Provincial Park boundary and within the mining claims, remains the preferred summer habitat of the migratory Fraser River sheep herd. The 1999 summer range locations for each of the 3 GPS collared animals concentrated in this sector. The lack of use of range within the park boundary may be a result of similar habitat use patterns of the small sample of collared animals, or may relate to some yet unrecognized attribute of the habitat in this particular area.

The migration routes recorded thus far have confirmed local knowledge of bighorn habitat use in some instances, and provided unexpected results in others. For example, the ram's migration route through the Edge Hills region has been known to locals for many years; however, the portion of the route through the Kostering Creek valley was new information to both locals and biologists. The timing of the migration in this case (10 November) was also surprising: migration out of the Marble Range was thought to be complete by the end of October.

The ewe's unexpected migration took her approximately 1 km north of the northernmost expected route. Knowledgeable residents were unaware that sheep used this area north of Barney Creek.

GPS location data have provided a graphic illustration of the migration behaviour of bighorn sheep of the Fraser River/Marble Range herd. Once migratory movements between seasonal ranges are initiated, it appears that the animals do not delay en route. Regardless of route location, migrating animals must cross a wide electrical transmission line right-of-way and a major road. In some locations, human habitation and large cutblocks must also be negotiated. The effect of these landscape features on migratory behaviour is presently unknown. Future work will address this issue through spatial analyses using digital orthophotograph coverage in a GIS environment. Location data collected in 2000 and 2001 may define currently unknown routes will further understanding of seasonal habitat use patterns and existing movement corridors.

MANAGEMENT CONSIDERATIONS

The die-off that seriously impacted the Fraser River bighorn population in the early 1990s has left the population at its lowest numbers in 20 years. Although the Marble Range sub-population was not affected to the same extent as the more northern sub-herd, the pneumonia-related lamb mortality was significant. Based on aerial survey data, this population is currently at 20% of the late 1980s estimate (B.C. Environment, unpublished data). Recent surveys indicate that lamb recruitment is rebounding, although total numbers do not appear to be increasing yet. The significance of important seasonal ranges and movement corridors, therefore, cannot be overstated. The protection of the remaining summer range in the southern Marble Range and the associated migration routes should aid in the recovery of the population to historic levels.

CONTINUING WORK

Currently, 2 GPS collars are deployed on rams captured on the Fraser River winter range. Following migration to the Marble Range in early to mid-June 2000, the collars will be released and the data offloaded and analyzed. The collars will be deployed once again on animals using the Marble Range prior to their migration to winter range in early November.

Ground inspection of the routes identified to date will be conducted during June 2000. Co-ordinates from the collar data will be input into hand-held GPS units and the routes covered on foot. Important terrain features, such as substrate, slope, and aspect will be documented and vegetation communities will be recorded for future analysis. Evidence of historical use (i.e. well-defined game trails) and pellet groups will also be recorded.

Upon completion of collaring efforts in the spring of 2001, all data will be collated and analyzed. Based on seasonal habitat use patterns, migration corridor definitions and requirements, recommendations for land use guidelines, specifically relating to mining operations and timber harvesting activities, will be developed and presented to local land use committees.

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EFFECTS OF PRESCRIBED GRASSLAND BURNS ON FORAGE AVAILABILITY, QUALITY AND BIGHORN SHEEP USE

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Abstract: We assessed the usefulness of prescribed grassland burns to improve bighorn sheep habitat in southwestern Alberta over a 4-year period (1994-1997). We conducted prescribed grassland burns in April 1995, 1996, and 1997. Burning decreased biomass of dead vegetation and increased live vegetation biomass. In all years, burning increased the crude protein content of vegetation up to mid-June. Protein content 1 year after the burn did not differ on burn and control plots. Bighorn sheep increased their use of burned areas by 2 to 5 times in spring and fall. There was no sex difference in the use of burn and control plots. In May, bite rates of sheep foraging on burns were higher than on controls, but in September bite rates were similar on burns and controls. On burns, males had a higher bite rate than females, while on controls females had a higher bite rate than males. There was no difference in fecal crude protein content of the forage selected by males and females. Grassland burns had a short-term positive effect on forage quality and probably improved sheep nutrition.

Keywords: foraging behaviour, forage quantity, quality, *Ovis canadensis*

In recent years, prescribed burning of grasslands and aspen (*Populus tremuloides*) has been used as a tool to improve habitat for ungulates such as bighorn sheep (*Ovis canadensis*), elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*) and to reduce the spread of trembling aspen (Stoeckeler 1960, Perala 1974, Svedarsky et al. 1986, Weber 1990, Peck and Peek 1991, Smith et al. 1999).

Bighorn sheep are mainly grazers, and rely on grassy south-facing slopes close to escape terrain, especially in winter (Shannon et al. 1975, Hofmann 1989). Grassy meadows that are not heavily grazed can accumulate a thick layer of dead vegetation, reducing the production of new vegetation each spring by preventing light from reaching the growing shoots. Dead grass is of poor quality and recent studies on bison (*Bison bison*), mule deer, white-tailed deer (*Odocoileus virginianus*) and bighorn sheep have shown that these ungulates preferred burned over control sites because burning increased diet quality (mainly protein content) and plant production (McWhirter et al. 1992, Shaw and Carter 1990).

Stelfox (1971) suggested that widespread wildfires around the beginning of the twentieth century resulted in higher-quality sheep ranges and therefore increased sheep numbers. Controlled burning of grasslands may therefore benefit ungulates by increasing biomass and quality of newly available forage (McWhirter et al. 1992). If controlled burning of grassland increased forage protein content and biomass, bighorn sheep should increase their use of burned sites. Little is known about the effects of controlled burning on bighorn sheep winter ranges and no studies have assessed how burns are used by different sex-age classes. It is also unclear whether any beneficial effects are long lasting or are limited to the year of the burn.

In an attempt to restore traditional grazing grounds for bighorn sheep, we carried out prescribed grassland burns on 3 different sites. We were interested in the effect of burning on the biomass and protein content of the forage available to bighorn sheep. Prescribed burns were performed in spring. We expected burned areas to offer new-growth forage earlier in the season and to produce forage of higher protein content compared to control areas, at least in the short term.

In observing the foraging behaviour of sheep, we tested how sheep habitat selection and foraging behaviour were affected by changes in forage quantity and quality on burned and unburned plots. We predicted that sheep would prefer burned plots over control plots and that sheep foraging on burns would have a higher bite rate than on the control because high quality forage is easier to process and more vegetation can be ingested per minute (Robbins 1993).

We also examined whether differences in sheep habitat selection changed seasonally with forage availability and quality. Finally, experimentally-induced variability in forage protein content was used to examine potential differences in foraging strategy of sheep according to sex. Several studies propose that females, due to their generally lower digestive efficiency compared to males and higher energy requirements during gestation and lactation, will be forced to select high-quality forage, while males do not face these constraints (see Main et al. 1996 for a summary). We therefore predicted that proportionally more females than males would use the burned areas, especially in spring when high protein forage is available. Consequently, fecal crude protein content was predicted to be higher in females than in males. Although we expected more females than males to prefer burns in spring (because of high protein content in the forage on the burn), we did not expect to find any sex-biased use of burns in September because protein content by that time would likely be low.

STUDY AREA

The Sheep River Wildlife Sanctuary was established in 1973 to protect bighorn sheep winter range in the foothills of the Rocky Mountains in southwestern Alberta (50° N, 114° W; 1420-1740 m. elevation). It includes open south-facing slopes and grassy meadows, intermixed with aspen copses and coniferous forest, mainly white spruce (*Picea glauca*) and lodgepole pine (*Pinus contorta;* Boag and Wishart 1982). The Wildlife Sanctuary is also an important winter range for elk and mule deer. In winter, the grassy slopes are frequently cleared of snow by warm Chinook winds, making forage easily available to ungulates.

During this study, all sheep (between 88 and 95 individuals) were either individually marked with plastic ear tags (98% of sheep) or recognisable by horn characteristics. Females and males used the same foraging areas in the Wildlife Sanctuary (Ruckstuhl 1998).

METHODS

Burns

The first grassland burn (Missing Link Mountain (MLFE), surface to be burned: ca.

100 x 50m, control surface 50 x 50 m) was done on 7 April 1995 on a south-facing slope at about 200 meters from escape terrain. The second burn (Hay Field, surface burned: ca. 150 x 250m; HF control surface: ca. 100 x 150m) was done on 29 April 1996 on a flat area, adjacent to escape terrain. The third burn, on a south-facing slope with adjacent escape terrain (Windy Point Mountain (WPE), surface burned: ca. 250 x 500m; the WPE control: ca. 100 x 150m), was done on 6 April 1997. Burn and control sites were chosen randomly, but adjacent to each other, with similar slopes, exposure and vegetation types. All 3 burns were situated within the Sheep River Wildlife Sanctuary on areas regularly grazed by bighorn sheep. The burn areas were surrounded by forest (WPE and MLFE) or cut off by a road (HF (north end) and WPE (south end)). Within each of these areas one side of the site was burned, the other left untouched. The burned areas were all large enough to attract groups of grazing bighorn sheep.

Bighorns were present (at least weekly) in all 3 years on all 3 sites in spring and fall. We limited our experiment to 3 different burns due to the following logistic problems: a)Fires had to be set by fire experts and needed the help of the Department of Forestry and the Department of Fish and Wildlife; b) A firefighter crew (at least 10 people) had to be present and ready in case the fire went out of control; c) Fires needed to be done at the right time, ideally, before spring green-up and when the ground was still a little wet from the snow melt; and d) Days with high wind speeds, which are common in the area, had to be avoided as potential days for burning. Due to these problems, only 1 burn was done in each year.

We monitored all burn and control sites from April to October 1994-1997 for sheep use, and each burn and control in the year of the burn and 1 year after for biomass production and protein content. Data from 1994 were used to control for site differences and time effects in sheep use and vegetation quality.

Forage quality and quantity

To estimate forage quality (percent crude protein) and quantity (biomass of dried vegetation) available to sheep, vegetation samples were collected from each burn and adjacent control site. At each site, 5 random samples (25x25 cm quadrates) of vegetation were clipped to the ground twice a month from May to July and once a month in August and September for a total of 8 sampling dates during each growing season (1995-1997). Samples were oven dried at 50^{o} C, weighed for total biomass, and later analysed for crude protein content with the Kjeldahl method (Robbins 1993). To measure the effect of burning on live biomass production, we separated the clipped vegetation of the MLFE burn in 1995 into dead and live forage.

Sheep use

Bighorn sheep used the Wildlife Sanctuary year-round, although in May ewes migrated to alpine areas about 12 km west of the Sanctuary to lamb. During summer they returned for short visits to the Wildlife Sanctuary, but were in the alpine areas most of the time until they migrated back to the Sanctuary in August and September (Festa-Bianchet 1986a, 1988; Ruckstuhl 1998; Ruckstuhl and Festa-Bianchet 1998). Although, in the past rams migrated to the alpine in summer (Festa-Bianchet 1986b), they apparently did not use the alpine areas during our study. Instead, rams often used low foothill areas east of the Wildlife Sanctuary.

To measure sheep use, burned and

control areas were searched daily. The location, time of day, and identification of all sheep were noted. The entire Sanctuary was censused once a week, to determine how many sheep were present. Sheep were generally easy to find in the Sanctuary (Festa-Bianchet 1986a). Fresh droppings left by individually known sheep were collected in April and May 1995 and 1996 to measure sexual differences in diet choice (fecal protein content). Fecal protein content was analysed using the Macro-Kjeldahl method (Robbins 1993). Sheep roamed freely and were feeding on other sites as well as on the burns. Therefore, data on fecal protein content will reveal the average diet choice by males and females regardless of the site they were feeding on. However, if females chose higher quality forage, it should be reflected in their fecal protein content.

Foraging behavior

In 1995 and 1996 we counted the number of bites sheep of both sexes took on the burn and control patches. For these observations, a focal animal was randomly chosen from a group of sheep grazing on either the burn or control. We counted the number of bites per minute during 10 1-minute focal samples. These 1-minute samples give a good estimate of the average number of bites taken by each individual per minute grazing.

Statistical analyses

All data were tested for normality and homoscedasticity using the SPSS statistical package (Norusis 1993). Non-parametric statistics were applied when data were not normally distributed and no transformation resulted in a normal distribution. As elevation, exposition and slopes are different for the 3 burns, data were analysed separately instead of in a multiple test. The effect of burning on vegetation protein content was thus analysed using Mann-Whitney U-tests, comparing control and burn plots for each of the different burn sites separately (Sokal and Rohlf 1995). All means are given with standard deviation.

Only a few sheep were found in the Wildlife Sanctuary between July and August. Hence, we only tested for sex-biased use of burn and control plots in April, May, and September when most rams and ewes were present. To describe seasonal sheep use of burn and control plots (independent of sex), we used the number of sheep observed on different plots per day, when sheep were present in the Wildlife Sanctuary. Differences in the number of individual sheep using burned and control plots each month were tested with Chi-square (Sokal and Rohlf 1995).

To correct for the higher number of females in the population, compared to males, we divided the total number of males or females that used a specific plot by the number of sheep of the same sex in the population for that year (excluding lambs). In 1994 we had 55 adult females, 35 males, and 5 yearlings. In 1995, the ratio was 54:37:11, in 1996 it was 51:36:7, and in 1997 the female, male, yearling ratio was at 36:36:16. We tested for sexual differences in plot use with Mann-Whitney U-tests (Siegel and Castellan 1988). Sexual differences in diet choice, measured as fecal crude protein content, were analysed with Mann-Whitney U-tests. Sexual differences in number of bites taken on burns and differences in number of bites taken on burns and controls were analysed using ANOVA.

RESULTS

Effects of burning on forage protein content and biomass

Prior to any of the burns in 1994, crude protein content varied seasonally, from May to by September, but was the same among the 3 burn sites (Kruskal-Wallis 1 way ANOVA (site as independent variable), χ^2= 0.38, df=2, *P*= 0.83). Crude protein content was highest in May and June with 12.9% (range 9.7-14.5% for all sites) and decreased to 7.0% (range 4.2-11.6% for all sites) by September.

Crude protein content of vegetation taken from the 1995 MLFE burn was higher than from the control from May to mid-June (*Z*= -5.41, *P*< 0.001, *n*= 40) (Figure 1). After June there was no significant difference in crude protein between the control and burn (*Z*= -1.34, *P*= 0.18, *n*= 120). Crude protein content decreased as the season progressed (Kruskal-Wallis 1-wayANOVA: χ^2= 73.83, df=4, *P*< 0.001, *n*= 160).

As with the MLFE burn, crude protein content of vegetation on the 1996 HF burn was higher than on control plots up to mid-June (*Z*= -7.40, *P*< 0.001, *n*= 85) (Figure 1). There was no difference in crude protein content of vegetation between burn and control from July through September (*Z*= -0.60, *P*= 0.55, *n*= 100). Protein content decreased during the summer (Kruskal-Wallis 1-wayANOVA: χ^2= 128.09, df=7, *P*< 0.001, *n*= 185). Crude protein content of the 1997 WPE site was higher on the burn than on the control up to August (*Z*= -3.99, *P*< 0.001, *n*= 30). The WPE was not sampled in May, but crude protein content in June was similar to crude protein content found on the MLFE burn and HF burn sites in burn years (10.4$\pm$1.2% on WPE burn; 7.0$\pm$1.1% on WPE control) (Figure 1). Protein content of vegetation in August was still high on the WPE burn (8.3$\pm$0.9%)

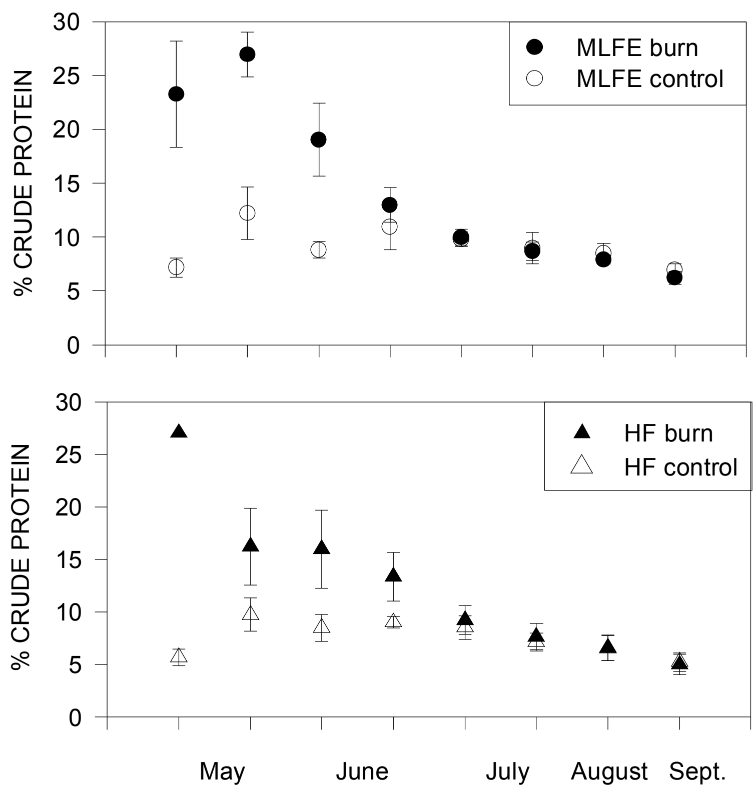

Figure 1: Percent crude protein content of vegetation of control and burn plots on the MLFE site from May to September 1995, and the HF site from April to September 1996. The MLFE site had been burned on April 7, 1995. The HF site was burned on April 29, 1996.

compared to the control (6.5±0.7%) (Z= -2.40, P< 0.05, n= 10).

One year after the burn at MLFE, crude protein (CP) content of vegetation on the burn had returned to pre-burn levels, with a yearly average of 6.2% CP and a range between 3.0% and 11.8% CP. Crude protein content on the control (10.0±1.2% CP) was higher than on the burn (7.0±1.0% CP) in July (Z= -2.95, P< 0.01, n= 20), but not in other months. Protein content decreased over summer (Kruskal-Wallis 1-way-ANOVA: χ^2= 44.18, df=7, P< 0.001, n= 80). The same pattern was observed for the HF burn. One year after the HF burn there was no difference in crude protein content on burned (8.0±1.8% crude protein, n= 10) and control (8.2±1.6%, n=10) patches (Z= -0.80, P= 0.43). Two years after burning crude protein content of vegetation on the MLFE site was higher on the control (7.0±0.4% CP) than on the burn (5.5±0.7% CP) in July (Z= -2.45, P= 0.014) but not in other months (highest Z-value= -1.78, P = 0.075, in August).

In 1995, burning resulted in lower total forage biomass on burns compared to controls up to August. In May, dry weights of vegetation samples taken from 25 x25 cm quadrats on MLFE were, on average, 10.1±1.1 grams for burn samples compared to 34.1±2.0 grams for control samples. By mid-August, total biomass of dried vegetation had reached control levels (both at 37.0±0.8 grams/25 x 25 cm). In September, biomass on burns was around 45.2±1.6 grams and on the controls 35.2+1.4 grams. A similar pattern was observed for the 1996 HF burn, where total biomass was practically zero after burning, but reached control levels by the end of July (Figure 2). One year after the MLFE burn, total biomass on burns and controls was similar (Figure 2).

In the year of the burn, biomass of live vegetation on the MLFE site was initially similar on the burn and control plots, up to August (Z= -1.27, P= 0.21, n= 36; Figure 3). While live biomass continued to increase up to September on the burn, there was a marked drop in live vegetation biomass on the control after August (Z= - 2.23, P<0.05, n= 35; Figure 3).

Effects of burning on sheep's plot choice and foraging behaviour

The sheep preferred to forage on new burns compared to control plots in all years (Table 1). All burns were done in April, and the MLFE burn produced only grass from May onwards, when the burn was preferred over the control site (Table 1). Sheep left the Wildlife Sanctuary in mid-to-late May but again used the burn extensively in September. The HF and the WPE plots were heavily used and were preferred grazing sites of sheep both in pre-burn and burn years. On the HF sheep preferred the burn plots over the control plots in all but 2 months of 1994 to 1996 (Table 1).

The number of sheep per day that used the different burn and control plots in pre- and burn years varied considerably between months (Figures 4-6). Sheep use was highest on all burns in spring, especially for HF (Figure 5) and WPE (Figure 6). The MLFE site was rarely used the year before and the year after the burn was done (Figure 4). The HF was still heavily used 1 year after the burn in 1997 and more sheep were on burn than on control plots (Table 1, Figure 5).

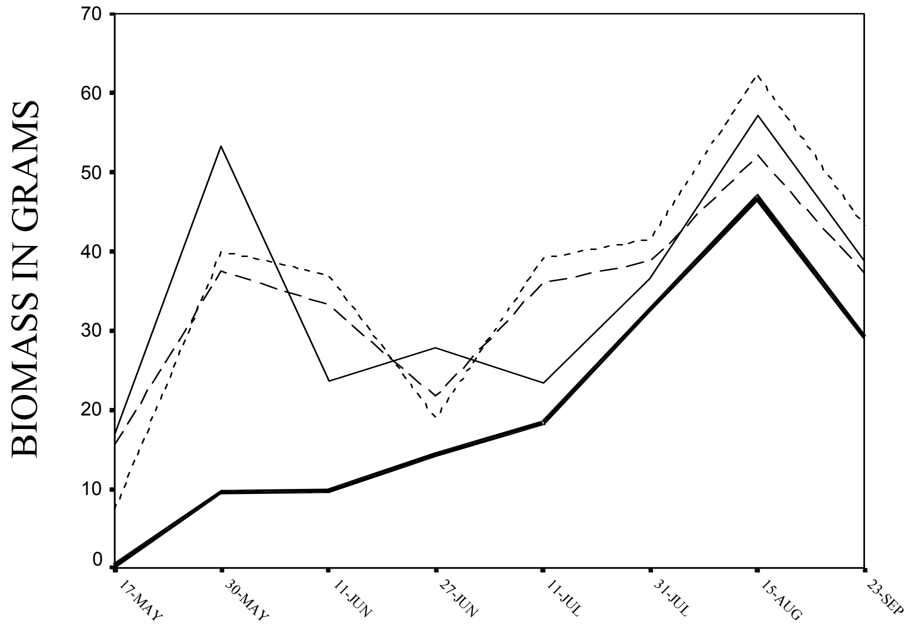

Figure 2: Dry weight of vegetation samples in grams, taken on HF and MLFE control and burn plots from May to September 1996. The HF site was burned in 1996 while the MLFE site had been burned the year before. ▬ = HF burn, - - - = HF control, — = MLFE burn, ---- = MLFE control.

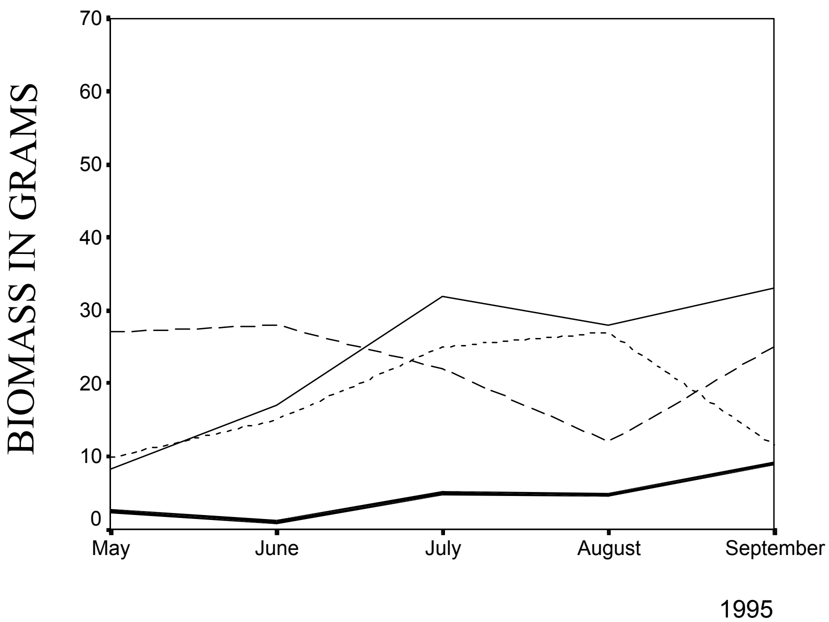

Figure 3: Dry weight in grams of dead and live vegetation taken on burned and control plots on the MLFE site from May to September 1995, the burn year. ▬ = dead vegetation on burn, − − − = dead vegetation on control. —— =live vegetation on burn, ... = live vegetation on control.

Table 1. Bighorn sheep use of burned and control plots the year before, the year of burning and a year after in the Sheep River Wildlife Sanctuary, Alberta, 1994 to 1997. Chi-square and P-values refer to the comparison of control and burned plots each month. Same = each sheep group seen used both the burn and the controls plots during observations; not used = plot was not used by sheep; n. s. = no significant difference between the use of burns and controls. χ^2-values in brackets = use of burn higher than of controls. Normal χ^2 = use of control plots higher than of burns. Rows with locations, years and statistics in bold indicate year of burning.

LOCATION & YEAR	APRIL	MAY	JUNE	JULY	AUGUST	SEPTEMBER
MLFE 94	Not used	Not used	Not used	Not used	Not used	Not used
MLFE 95	**Not used**	**(χ^2 = 224) P<0.05**	**Not used**	**Not used**	**Not used**	**(χ^2 = 27) P<0.05**
MLFE 96	Not used	(χ^2 = 7) P<0.05	Not used	Not used	Not used	Not used
MLFE 97	Not used	Not used	Not used	Not used	(χ^2 = 20.4) P<0.05	(χ^2 = 18) P<0.05
HF 94	χ^2 = 0.65 n. s.	χ^2 = 1.1 n. s.	(χ^2 = 25) P<0.05	(χ^2 = 29) P<0.05	(χ^2 = 18) P<0.05	(χ^2 = 65) P<0.05
HF 95	(χ^2 = 72.7) P<0.05	(χ^2 = 214) P<0.05	(χ^2 = 26.5) P<0.05	(χ^2 = 8) P<0.05	χ^2 = 30.9 P<0.05	χ^2 = 5.2 P<0.05
HF 96	**(χ^2 = 54) P<0.05**	**(χ^2 = 5) P<0.05**	**(χ^2 = 7.2) P<0.05**	**(χ^2 = 31) P<0.05**	**(χ^2 = 284.1) P<0.05**	**(χ^2 = 56.5) P<0.05**
HF 97	(χ^2 = 79.1) P<0.05	(χ^2 = 84.1) P<0.05	(χ^2 = 11) P<0.05	(χ^2 = 54.01) P<0.05	(χ^2 = 192.2) P<0.05	(χ^2 = 6.1) P<0.05
WPE 94	Same	Same	Same	Same	Same	Same
WPE 95	Same	Same	Same	Same	Same	Same
WPE 96	Same	Same	Same	Same	Same	Same
WPE 97	**Same**	**(χ^2 = 20.3) P<0.05**	**(χ^2 = 23.3) P<0.05**	**(χ^2 = 53) P<0.05**	**Same**	**(χ^2 = 58) P<0.05**

In April and May of the burn years, on average 13% of all females (interquartile range = 24.9%; min. = 0%; max. = 70.8%) and 11.1% of all males (interquartile range = 20.8%; min. = 0%; max. = 62.2%) used the burns. In September on average 12.5% (interquartile range = 24.3%; min. = 2.0%; max. = 66.7%) of all females and 12.8% (interquartile range = 9.0%; min. = 0%; max. = 23.9%) of all males used the burns. There was no sex-biased use of the different burns in April, May or September (largest *Z*-value = -1.54, *P*= 0.12, *n*= 32 days, in spring on WPE).

There was no sexual difference in diet choice in 1995 or 1996 (*Z*= - 1.39, *P*= 0.17, *n*= 113 sheep). Fecal crude protein content was on average 14.1±4.2% for females and 15.7±5.3% for males. There was, however, a significant difference in overall fecal protein content between the years 1995 and 1996. In 1995, fecal protein content was much higher than in 1996 (*Z*= -6.90, *p*< 0.001, *n*= 113, Table 2).

In May when sheep use of the burns was greatest, they took on average 50±1 bites/min (*n*= 32 sheep) when grazing on the control and 56±2 bites/min (*n*= 20 sheep) when grazing on the burn plot. In autumn bite rates were similar on burn and control plots (respectively 41±1 bites/min and 43±6 bites/min, *n*= 20 sheep in each case, *F*= 2.72, *P*= 0.133). Over the entire summer, grazing sheep took more bites per minute on burns than on controls (*F*= 11.59, *P*< 0.01, *n*= 52 individuals). Surprisingly, in spring, males took more bites per minute than females on the burns (males: 59±1 bites/min, n = 22, females: 53±2 bites/min, n = 18; *Z*= - 2.51, *P*<0.05). The opposite was observed on controls, where females took more bites per minute than males (males: 49±1 bites/min, *n*= 38, females: 52±1 bites/min, *n*= 26; *Z*= - 2.16, *P*< 0.05).

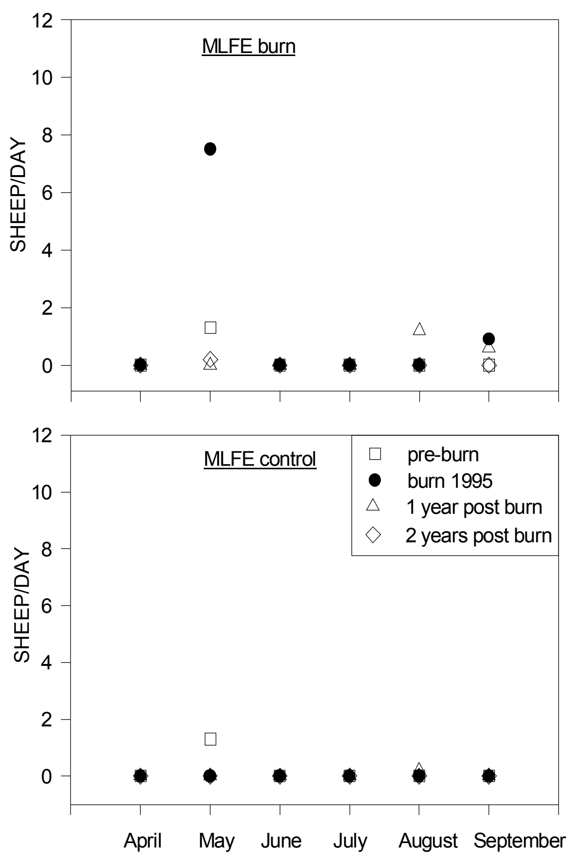

Figure 4: Observed average daily sheep use of the MLFE burn and control plots 1 year before, the year of the burn, 1 and 2 years after the burn (1994 – 1997). The MLFE site was burned on April 7, 1995.

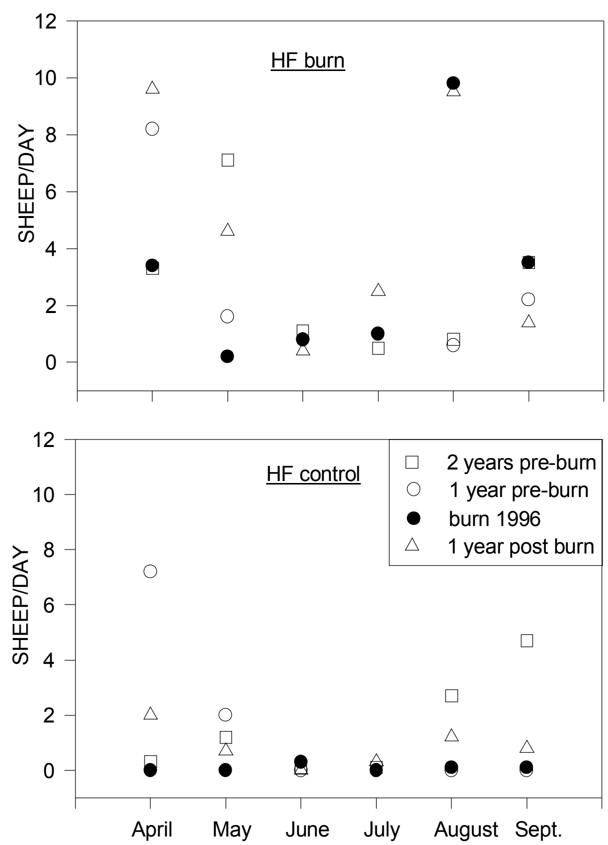

Figure 5: Observed average daily sheep use of the HF burn and control plots 2 and 1 years before, the year of the burn and 1 year after the burn (1994 – 1997). The HF site was burned on April 29, 1996.

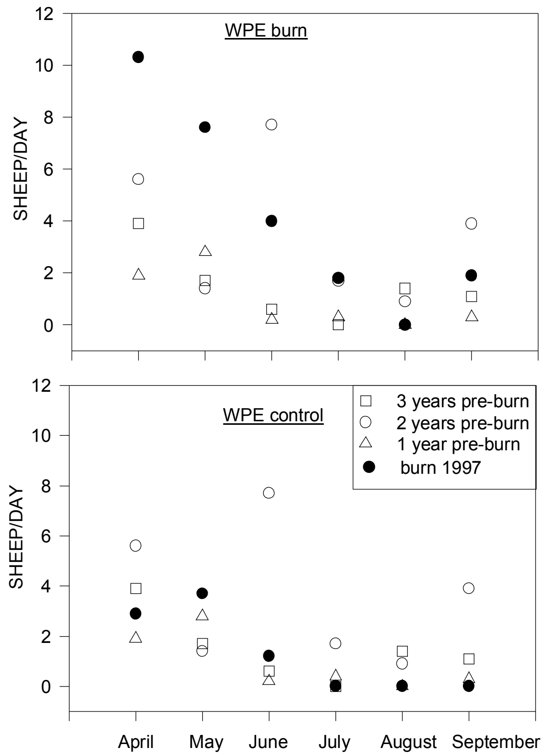

Figure 6: Observed average daily sheep use of the WP burn and control plots 3 to 1 years before and the year of the burn (1994 – 1997). The HF site was burned on April 6, 1997.

Table 2: Average percent of crude protein content found in feces of male and female bighorn sheep in spring 1995 and 1996, in the Sheep River Wildlife Sanctuary, Alberta, Canada. SD = Standard deviation of mean.

SEX & YEAR	% FECAL PROTEIN	SD	N	MEDIAN
Females 1995	18.34	2.98	20	18.86
Males 1995	20.24	3.97	20	20.25
Females 1996	11.51	2.34	33	11.48
Males 1996	13.39	4.27	40	12.47

DISCUSSION

From May to mid-June, the crude protein content of vegetation was much higher on burned than on control plots, but after mid-June burning had little effect on crude protein content. A seasonal effect of burning forage on crude protein content has also been reported by previous studies. Carlson et al. (1993) found that burning of Key woodland habitat in Florida increased the protein content of browse available for white-tailed deer (also called Key deer), especially in May, June, and July. McWhirter et al. (1992) reported that forage on burned grassland-brush sites had a significantly higher level of protein content than control sites each spring, and concluded that the benefits of burning lasted a minimum of 15 years, in terms of food availability and composition. Apparently, bighorn sheep living in their study area preferred burned plots to controls each year during spring (McWhirter et al. 1992). Hobbs and Spowart (1984) burned grass and brush communities and found that the effects of burning on forage crude protein lasted for at least 2 years, primarily due to a diet switch by animals grazing on the burn. In the Hobbs and Spowart (1984) study green grass was more abundant and nutritious (often exceeding 25% crude protein) on burned than control plots during winter, and the proportion of green grass eaten by an ungulate therefore increased the quality of its diet. In our study area there was no green grass available for ungulates during winter. Little annual variation exists in the timing of spring green-up due to the strongly seasonal climate. Furthermore, our study differs from Hobbs and Spowart (1984) in that we did not measure the protein content of separate plant species, rather we measured the overall protein content of all available vegetation for sheep. We could, therefore, demonstrate only a short-term increase in forage quality: forage protein 1 and 2 years after burning was not higher on burned than on control plots. Differences in sheep use of burned versus control sites over time also demonstrated the short-term benefits of grassland burns in northern climates. For example, sheep preferentially used the MLFE burn in spring and fall of the burn year, but not the year after.

It is not clear why burning had only a short-term effect on crude protein content or biomass production. Possibly, because especially grass biomass production in this area is generally high, dead vegetation had already accumulated by the first spring following the fire. A new layer of dead grass therefore could inhibit vegetation growth in the second year. Similarly, Seip and Bunnell (1985) found no difference in crude protein content of vegetation between burned and unburned Stone's sheep (*Ovis dalli stonei*) ranges during or after the year of a burn, although they stated that, in May, burned slopes provided more new forage for sheep than unburned slopes.

In our study, new forage on burns had a much higher crude protein content and was more accessible as it was not hidden by old growth. Many studies show a clear tendency for ungulates to prefer newly burned foraging plots over unburned ones (Hobbs and Spowart 1984, Shaw and Carter 1990, McWhirter et al. 1992, Coppedge and Shaw 1998). Preference for burns over controls is most likely due to 2 factors: the much higher level of crude protein usually found in new growth and the sometimes earlier availability (Hobbs and Spowart 1984) of new growth compared to controls. Burning therefore benefits sheep and other ungulates because it enhances forage quality.

Total biomass of forage available on burns, in our study, was not higher than on controls but new-growth forage on burns was more accessible than on controls. Not surprisingly, sheep preferred burn to control sites in all 3 years of our study. The MLFE site attracted bighorn sheep after burning until mid-June, which indicates that sheep selected this area because of the burn. Sheep did not usually use the MLFE burn or control sites during the years before or after the burn, again a clear indication that sheep were attracted to the site because of the burn. However, the WPE and HF sites were preferred grazing areas of sheep even before any burns were done: the HF burn site, for instance, was preferred over the HF control site even in pre-burn years. It was therefore difficult to determine whether sheep used the HF burn because they profited from higher quality forage or because they merely preferred the location, which coincided with the burn. Based on the sheep use on MLFE and WPE, which was highest in burn years, we conclude that sheep used the HF burn because of its higher protein content and not solely because it was a preferred site. Our burned plots were larger than the control plots, and burn plots may hence be expected to receive more sheep use than the control plots if sheep were distributed at random (see also Coppedge and Shaw 1998). If this was the case however, these differences in sheep use should have been seen every year. Instead, the WPE and MLFE burned plots were preferred only in the years of burning.

Sheep were using the high quality forage in May but less so in June, when the protein content was still much higher, mainly because females migrated to alpine areas after mid-May and rams moved east of the Wildlife Sanctuary. By the end of May in 1996, there were almost no females and sometimes only a few males left in the Sanctuary. Females moved back into the area in September, which explains the preferential use of burn plots in September and no use from June until September. Therefore it appears that burning affects site selection of bighorn sheep within a given seasonal range, but does not affect their seasonal migratory patterns. By September, crude protein content was similar on burned and control sites, but there was more live forage available on burns than on controls, because of dead grass accumulation on controls.

We expected that the increased biomass and quality of new vegetation would allow sheep to take more bites on burned plots than on controls. Bite rates were higher on the burns than on the controls in May but not in September. In another study (McWhirter et al. 1992), both bite rates and the time spent feeding on burns were significantly greater than on controls. Shaw and Carter (1990) reported that bison foraged at a disproportionately high rate on a grassland burn, but use declined gradually as summer progressed. The higher bite rate in May during our study is likely due to the fact that newly emerging forage in spring is short and faster to ingest and process than old vegetation. Sheep feeding on the burn would therefore be able to take more bites than on controls.

Contrary to our findings, Seip and Bunnell (1985) found no difference in bite rate of Dall's sheep feeding on burn or control patches. The number of bites an ungulate takes depends on several factors, such as bite and rumen size, plant structure and size, chewing and processing constraints, and availability of forage (Illius and Gordon 1992, 1993; Gross et al. 1995; Gordon et al. 1996). That Seip and Bunnell (1985) found no difference in bite rates on burns and controls could therefore be due to several factors. Sheep on burns and controls might have foraged at their maximum intake rate (if biomass in general was low on both sites). Total biomass availability could have been the same on both plots, which results in the same number of bites (independent of the proportion of dead versus live vegetation available per bite). Finally, sheep on burns might have taken more steps while foraging, decreasing bite rate.

Surprisingly, males took more bites per minute on the burns than females, while females took more bites than males on the controls. Smaller individuals may take more bites to compensate for their smaller incisor bar size, so it is not really surprising that the smaller bighorn sheep females took more bites than the larger males (Gross et al. 1995). In late April and early May, new growth on burns was just beginning to emerge. The relatively short size of the forage could therefore explain why males took more bites than females. On normal-height vegetation, large males, with their larger mouths, have a relatively bigger intake of food than females but this may be more difficult to achieve at very short forage heights. They therefore may need to increase their bite rate to achieve the same total intake as on taller vegetation.

Contrary to our predictions, there was no sex difference in burn use, which suggests that both males and females benefited from higher quality forage in spring. Furthermore, there was no sexual difference in diet choice, reflected by fecal crude protein content of the forage. Although some studies have supported the hypothesis that females opt for higher quality forage than males, others found no difference or the reverse (Main et al. 1996). To our knowledge, only Coppedge and Shaw (1998) examined the effects of sex on use of burns. The authors found that bull groups showed less attraction to burned areas than female groups, supporting the hypothesis that the smaller females should opt for high quality forage while the larger males do no not need to do so (Main et al. 1996). Our results indicate that there is no sexual difference in diet choice in bighorn sheep, although the larger males had a slightly higher fecal protein content than the smaller females. If forage is of higher quality, or is accessible earlier in the season, males may select these areas, and hence recover earlier from energy loss (due to the winter and the rut), and therefore increase their body condition and chance of survival. Gravid females will have a higher protein supply to satisfy the energy demands of their last month of gestation. Both males and females therefore can profit from late winter/early spring burning of grassland.

As shown by this study, there is a direct link between burning grassland patches and the increase in forage quality and sheep use of such patches, at least for the year of the burn. Annual grass burns should be done early in the year (preferably between February and mid-April), when snow in the forests can minimise the danger of fire escaping the prescribed boundaries. Burning grasslands could then be used as a useful, and sometimes inexpensive management tool to increase bighorn range quality in key areas.

Increasing range quality would likely lead to population growth or to sheep in better body condition. Prescribed burning of grasslands could, therefore, not only profit bighorn sheep but likely other grazing ungulates (mainly elk, white-tailed and mule deer) sharing the same habitat. The burns should ideally be planned and conducted to closely match the known natural fire rotation period for the particular ecosystem where the bighorn sheep or other ungulates under consideration live. In taking these rotation periods into account, vegetation type conversions or the loss of local plant species due to too frequent burning can be avoided.

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THE USE OF VIDEO FOR MOUNTAIN GOAT WINTER RANGE HABITAT INVENTORY AND ASSESSMENT OF OVERT HELICOPTER DISTURBANCE

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Abstract: During the winters of 1997-2000 we conducted 39 helicopter surveys throughout the Sunshine Coast area of British Columbia to identify coastal mountain goat (*Oreamnos americanus*) winter range habitat. We also conducted 4 ground surveys to support the aerial survey program. We confirmed that coastal mountain goats used mature coniferous forest for snow interception cover, bedding, and foraging habitat. A total of 716 mountain goat sightings were classified; 58% of the total animals sighted were captured on video. Each video clip was analyzed as a separate “sighting event” to remove the influence of group size. The video data was used to document overt mountain goat helicopter disturbance response, winter association with forested stands, and to assess the effectiveness of video as a wildlife inventory tool. We noted a high degree of mountain goat association with forested cover during our winter flights; 72% of all sighting events were associated with non-productive or productive forest stands. Mountain goats showed a moderate-to-extreme overt response to the helicopter in 73% of the sighting events captured on video. We found video to be a very useful tool for determining mountain goat helicopter disturbance response, use of habitat components and for ongoing habitat classification.

Key words: forest association, snow interception, *Oreamnos americanus*, overt disturbance, sighting event, Sunshine Coast, ungulate, video, winter range habitat.

In British Columbia, ungulate winter range habitats have been recognized as a resource feature requiring special management under the Forest Practices Code of B.C. Act. Coastal mountain goats are thought to be particularly dependent upon stands of snow interception forest for their winter survival due to the heavy, persistent snowpack typical of coastal ecosystems (Hebert and Turnbull 1977). Southerly aspect, closed canopy forested stands associated with suitable escape terrain are required to provide both snow-free refugia and foraging opportunities during heavy snowfall events. Focusing on mountain goat winter range habitats in the Sunshine Coast, we undertook 4 years of intensive winter helicopter surveys to identify winter range habitats, assess mountain goat use of habitat components, and to document the overt disturbance responses of mountain goats sighted during the inventory program. Funding was provided through Forest Renewal British Columbia and the Common Land Information Base for the Sechelt and Homalco First Nations traditional territories.

STUDY AREA

Located on the southwest mainland coast of British Columbia, the Sunshine Coast is an area of complex topography within the Coast and Mountains Ecoprovince, and includes portions of the northern and southern Pacific Ranges, Outer Fiordlands, and Georgia Depressions ecosections (Demarchi 1995). The complex, mountainous topography and associated high rainfall result in a very diverse climate and ecology, which is expressed in a variety of ecosystems from nutrient rich, moist valley bottoms and productive river estuaries to high elevation alpine meadows. The majority of the area experiences a significant snowpack during most winters with wet coastal snow often persisting through the winter months from as early as October through to April in many areas. Mountain goats are widely distributed throughout the Sunshine Coast and are closely associated with habitat complexes that include both escape terrain and forested stands.

METHODS

Survey methodology was consistent with the Resource Inventory Committee (1996) population presence/absence aerial ungulate survey methodology. Individual mountain goats were classified using binoculars and video magnification to identify physical characteristics outlined by Chadwick (1983) and Smith (1988). Surveys were conducted from January through March when mountain goats are typically concentrated on their winter range habitats. Video footage was captured for all survey transects for post-flight review.

The location and elevation of animal and track sightings were recorded using helicopter Global Positioning System (GPS) according to longitude and latitude or UTM co-ordinates. Elevations were recorded in feet above sea level using the helicopter gauges during flights and converted to meters above sea level when transferred to Terrain Resource Inventory Maps (TRIM) upon completion of flights. Continuous video footage was captured for all survey transects using hand-held video cameras. We used helicopters fitted with photo doors whenever possible to aid video capture. Audio commentary was recorded using a variable rheostat resistor to filter helicopter turbine noise. The elevation, GPS position, age/sex class of all animals observed and their responses to the helicopter were recorded both on video audio commentary and flight data forms. A video summary tape was prepared by collating all survey tapes chronologically and re-recording all visible mountain goat sightings in VHS format. Each video clip was assessed as a separate sighting event to remove the influence of group size.

RESULTS

Age/sex classification

A total of 716 individual mountain goats were classified (Table 1). " Adults" included unsexed goats confirmed as adults due to their size only. When adults could be visually sexed, they were separated into male and female classes. Adult "males" were generally classified with confidence due to their physical size and solitary nature. "Females" usually occurred in nursery groups with "kids" (animals less than 1 year old) and "yearlings" (animals between 1 and 2 years of age) which were distinguishable by their relative size and horn development. Solitary animals were classified as females only if horn shape was clearly visible in flight or on the video footage. Adults in nursery groups were classified as females with a high degree of confidence based on existing knowledge of goat habitat use and behaviour (Foster

1982, Chadwick 1983, Stevens 1983, Shackleton 1999).

Table 1: Age/sex classification of mountain goat observations (n = 716).

Survey Year	Male	Female	Yearling	Kid	Unclass-ified	Adult
1997 (n = 173)	9	42	17	28	57	20
1998 (n = 344)	16	62	47	43	77	99
1999 (n = 83)	11	20	5	10	14	23
2000 (n = 116)	14	21	17	4	31	29

Habitat use

Past surveys in the Sunshine Coast found preferred mountain goat winter range habitats ranged from 300 to 1000 m in elevation on predominantly southerly aspect cliff/bluff/gully complexes (Morgan and Forbes 1982). We found goats occupying habitats between 200 and 1500 m above sea level in elevation in our study area (Fig. 1). The majority of goat sightings occurred between 751 and 1250 m in elevation. We found limited use of habitats below 500 m, though use of low elevation areas was documented adjacent to lakeshore and marine foreshore habitats. Low elevation habitats were typically occupied by nursery groups. Adult male mountain goats appeared to use higher elevation, northerly aspect habitats to a greater degree than females and nursery groups. The elevation of goat sightings in our study area is generally lower compared to sightings recorded in interior ecosystems in adjacent Districts. Ongoing analysis of habitat polygons identified through our survey program according to slope, aspect and elevation classes is occurring.

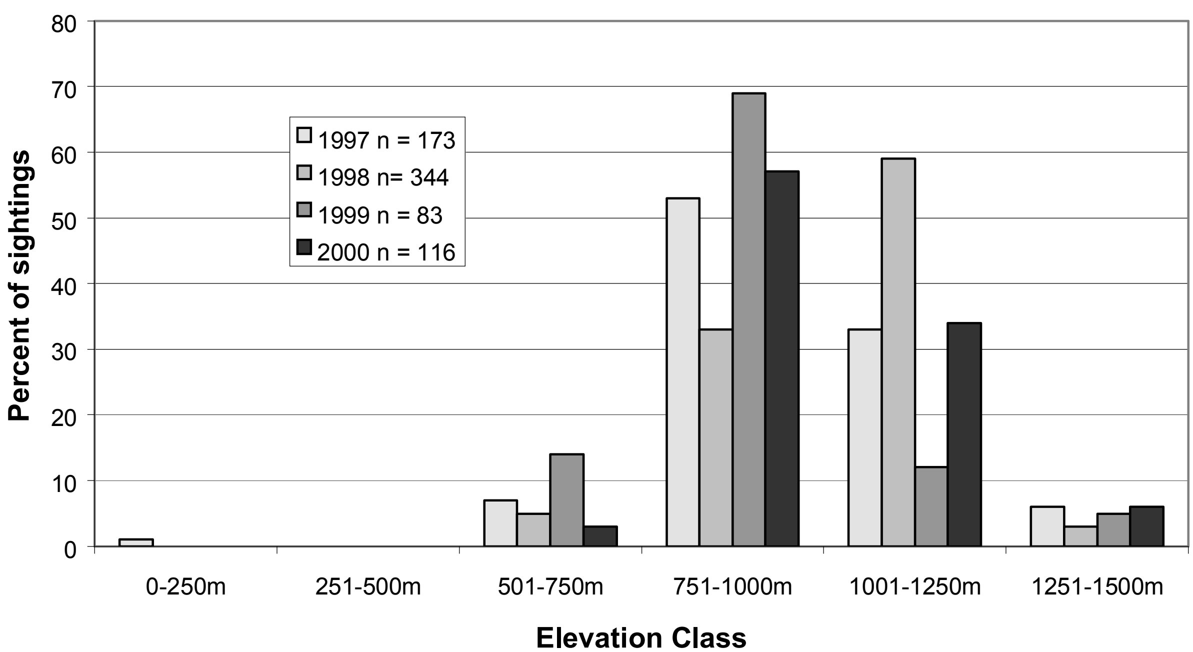

Fig. 1. Elevation classes of goat sightings 1997 – 2000 (n= 716).

Video analysis

We attempted to capture all sightings on video during our survey flights. One hundred and seventy-five video clips with visible mountain goats were captured; each clip includes a single sighting event with variable numbers of individual animals visible. The video data set was used to assess goat disturbance response to helicopters and to assess their use of forested areas in winter. Success capturing goats on video varied from year to year (Table 2).

Table 2. Video success by survey year. The number of sighting events captured on video compared to total number of sighting events has not been calculated.

Year	1997	1998	1999	2000	Total
No. Animals sighted	173	344	83	116	716
Total Video Capture (No. animals)	73	258	26	58	415
Video Success	42%	75%	31%	50%	58%

Forest Association

Mountain goat use of forested stands was documented throughout the study area by review of the 175 sighting events captured on video (Table 3). Our aerial surveys confirmed mountain goat use of structures such as individual large diameter old-growth coniferous trees, hollow snags and mature forested stands in winter. Our ground surveys also confirmed mountain goat use of these habitat components. We classified video clips according to 4 categories: productive forest (areas containing stands of large coniferous trees), non-productive forest (short trees, scattered distribution, low volume stands), non-productive scrub (areas with no large coniferous trees, woody vegetation limited to small shrubs or deciduous stems), and non-forested areas. Sighting events were associated with forested stands if such habitat occurred within estimated 50 horizontal meters of a given mountain goat sighting.

A total of 72% of the video clips (sighting events) were associated with productive or non-productive forested stands.

Table 3. Mountain goat forest association (n= 175).

Forest Category	No. of video clips	Percent of video clips
Non- forested	7	4%
Non-productive scrub	42	24%
Non-productive forest	68	39%
Productive forest	58	33%

Helicopter Disturbance

The set of 175 video clips was also used to assess the level of mountain goat disturbance according to visible criteria. Five classes of overt response to helicopter disturbance were used for analysis:

EXTREME - Panic: animals scattered and ran for duration of sighting.

HIGH – Animals ran, sought shelter, obvious disturbance.

MODERATE – Visible fright response (tail raised). Animals walked to shelter, hid.

LOW - Interrupted foraging/ruminating, increased vigilance. Animals observed the helicopter and stopped foraging or bedding (did not walk or run).

NIL - No visible overt response (animals remained bedded, continued foraging)

Physiological stress was not assessed but is expected to be significant in all overt reaction classes (Joslin 1986*a*, Frid 1997).

Only 5% of all sighting events showed a "nil" overt disturbance response and 22% of sighting events showed a "low" overt response. Thirty-three percent of the video clips showed a moderate disturbance

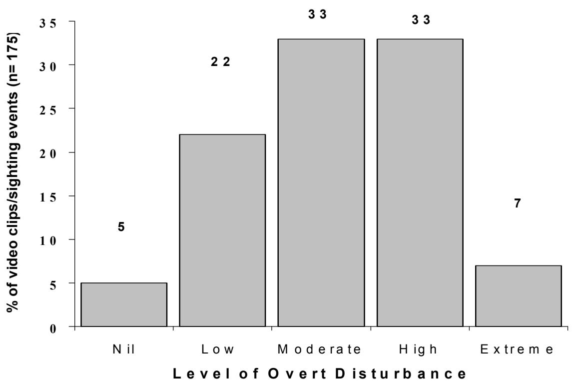

Fig. 2: Level of Overt Disturbance vs. % of sighting events .

response, 33% a high disturbance response and 7% an extreme response. Combining the moderate to extreme disturbance classes results in 73% of clips indicating a marked overt disturbance response to helicopter activity. We conducted surveys as close to the hillside as practical to maximize track visibility within forested stands; the distance from the helicopter to the hillside thus varied during surveys due to topographic constraints and our efforts to minimize goat disturbance and duration of exposure. Based on our aerial observations there does not appear to be a consistent relationship between goat overt disturbance response and the distance to the helicopter.

Goats exhibited a greater overt disturbance reaction to helicopter presence if overhead shelters such as caves, ledges, or large conifer trees with low-lying boughs were not available; goats used such features to hide from the helicopter whenever available and accessible. Higher overt disturbance levels were noted when the helicopter was above or level with the relative position of mountain goats on the hillside. Lower overt disturbance responses were noted when the helicopter was below the relative position of goats sighted. Females with kids (nursery groups) showed the highest levels of overt reaction to helicopter presence while adult males (billies and lone adult goats) appeared to be disturbed to a lesser degree. We assessed the percent of encounters of each class of goats vs. overt disturbance rather than the number of animals, to remove the influence of sample size (Fig. 3).

Four ground surveys were conducted to support the aerial survey program. During ground surveys, we noted noise levels were much higher when the helicopter was above our position on the ground. Noise levels were notably reduced when the helicopter was below or level with our position. The extreme terrain occupied by goats and limited access restricted our ground surveys to relatively subdued winter range habitats. Egress points were limited to areas with large ledges and meadows.

DISCUSSION

Video Analysis

Track sightings in snow often indicated mountain goat movement between forested and non-forested habitat components and were recorded on the audio commentary. Tracks were often not visible on the video clips. We intend to further review the audio commentary to include mountain goats' use of forested stands not visible on the video clips in the forest association analysis. We found video very useful for assessing mountain goat overt disturbance reaction to helicopter activity, for quantifying mountain goat use of forested stands in winter, and for cataloguing winter range habitats for future management applications. The use of video enabled us to maximize information obtained during each survey by facilitating ongoing review of 175 sighting events. For example, we may be able to further refine our categories of forested stands to include such variables as the amount of arboreal

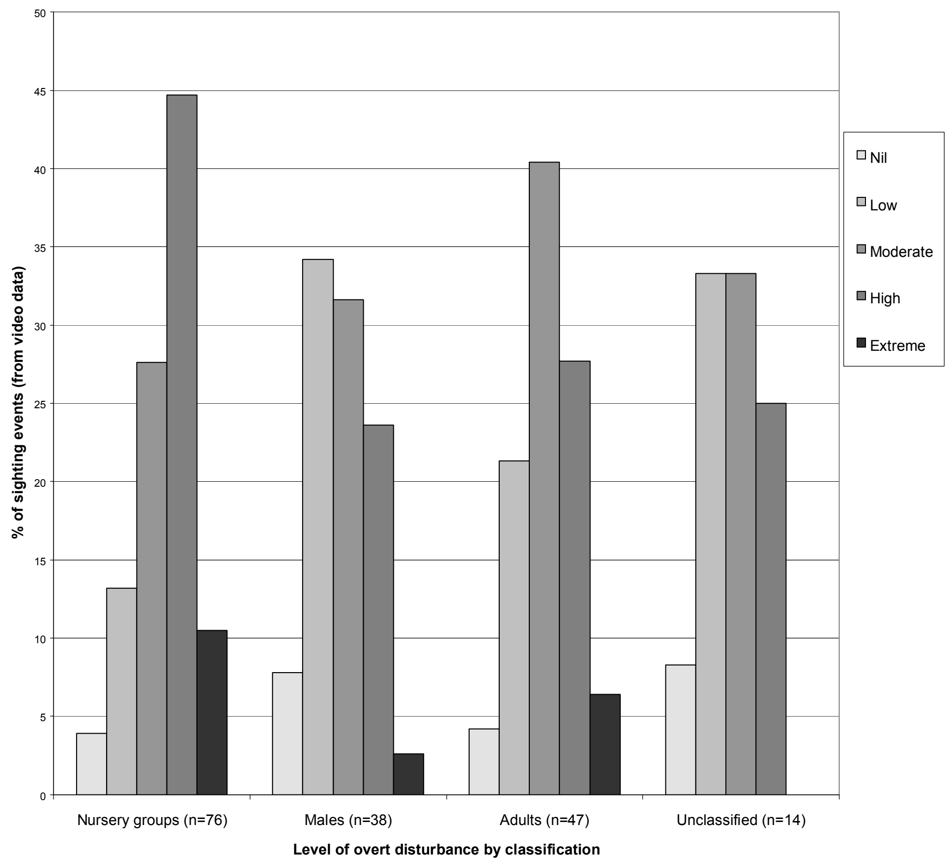

Fig. 3: Level of overt disturbance vs. grouped age/sex class of mountain goats (n= 175)

lichen (*Alectoria* spp.) and presence of large-diameter old growth trees.

While we expected video success to increase as the survey program proceeded, we noted poor results in 1999 relative to other years of the survey program. This may be due to inclement weather and deep snow conditions that occurred during the winter of 1998/1999.

Use of digital video allowed capture of footage up to 120 times magnification but the utility of the higher magnifications was often limited by helicopter vibration. Video footage provided useable images of physical characteristics such as horn shape, leggings, relative size, and face shape (Chadwick 1983, Shackleton 1999) for confirming age/sex classification in many cases. Ongoing review of the video footage may enable us to quantify the degree of error in flight classification of individual animals or define classification uncertainty.

Video capture has also allowed us to develop a comprehensive visual record of habitat complexes throughout the study area. Still images will be extracted from the video in order to catalogue winter range habitats identified during our surveys programs, facilitating detailed descriptions of each area for management applications.

Helicopter disturbance

Helicopter disturbance can result in significant effects on mountain goats, including interrupted foraging, physiological stress and reduced vitality due to increased energy expenditure, increased metabolic rate, and reduced time foraging (Chadwick 1983, Joslin 1986*b*, Côté 1996, Shackleton 1999). Chadwick (1983) noted slowed chewing rates and interrupted rumination associated with logging and road building in Montana. Joslin (1986*b*) found peaks in seismic exploration activity coincided with declining adult female numbers, kid numbers and reduced reproductive success in a radio telemetry study in Montana. In the high to extreme disturbance classes (40% of the total sighting events on video) significant energy expenditure was evident through flight responses with goats running or obviously stressed due to helicopter presence. Given the extreme terrain typical of mountain goat winter range habitats, we consider goats at increased risk of falling or injury in the moderate to extreme overt disturbance classes; 73% of the 175 sighting events were classed as moderate to extreme overt responses. The level of physiological disturbance was not determined. Actual physiological stress levels in the nil to low overt response classes may be significant and result in detrimental effects on goats (Joslin 1986*b*, Côté 1996, Frid 1997). Though increased vigilance of mountain goats was classified as a low overt disturbance in our study, it may be indicative of increased physiological stress. We consider our overt disturbance classes to be conservative estimates of helicopter disturbance levels; total stress is likely under-estimated.

Habitat abandonment by mountain goats has been previously documented; Foster and Rahs (1985) noted temporary abandonment of summer ranges in northwestern B.C. due to hydroelectric exploration activities. The potential for abandonment of home ranges by mountain goats due to chronic disturbance is supported by our observations of goat habitat occupation in the Jervis Inlet portion of our study area. The results of aerial inventories, operational flights and anecdotal observations indicate decreased goat use of previously occupied habitats subsequent to sustained helicopter logging in close proximity. This may be due to habitat alienation from timber harvesting, habitat abandonment in response to sustained helicopter disturbance, or a combination of factors. It is unclear whether increased mortality or habitat abandonment has resulted from industrial helicopter logging disturbance, however, re-occupation of previously occupied habitats has not been confirmed. No increase in goat density was noted in adjacent winter range habitats, which would have indicated movement of animals from disturbed areas to alternate habitats. Alienation of goats from historically occupied habitats is also suspected based on flight results in the nearby Squamish area (S. Rochetta, B.C. Ministry of Environment, Lands and Parks, personal communication). The causal factors for reduced goat sightings in areas with recent high intensity helicopter activity have not been determined. Historic mortality due to hunting, increased road access and disturbance by industrial activity may be factors contributing to the reduced levels of mountain goat occupation noted.

Since mountain goats, like other ungulates, are in poor physical condition during the winter and at highest risk of mortality due to falling, starvation or other factors, care must be taken to reduce stress on animals during surveys and any activities adjacent to occupied winter range habitats (Frid 1997). As surveys must be conducted close to the hillside to obtain track sightings, we attempted to minimize total exposure time and to distance the helicopter from the animals immediately after a confirmed sighting to reduce disturbance.

We attempted to estimate the distance of goats from the helicopter during surveys and via review of the video footage. Distance was difficult to estimate as the relative position of the helicopter to the ground constantly changed. In most cases, the level of disturbance observed increased as the distance to the helicopter decreased, though this does not appear to be a consistent relationship. In some cases, a low level of overt response was evident when the helicopter was in close proximity to individual goats. Conversely, high overt disturbance reactions were noted in several cases when the helicopter was a kilometer or more from the goats. The results of our video analysis indicate a higher degree of overt disturbance by nursery groups compared to solitary adult animals or bachelor groups of adult male goats (Fig. 3). This contrasts with the results outlined in Côté (1996) which indicated no apparent difference in the level of reaction to helicopters between bachelor or nursery group types. We found a generally higher overt response to helicopters by nursery groups throughout the study, though we were only able to assess the responses captured on the video data set (n=175 clips/ 415 animals). Frid (1997) hypothesized that animal-related variables such as group size, composition and pre-disturbance activity may interact to affect the strength of a disturbance reaction; our results appear to support this hypothesis. The relative elevation of the helicopter also appears to be a factor affecting overt disturbance response. Foster and Rahs (1985) noted accentuated stress responses to helicopters when the disturbance was above or level with a particular animal; our observations are consistent with this finding. We found goats consistently responded more dramatically to helicopter presence when the helicopter was above their position. Our ground surveys confirmed noise levels were lower and mountain goat overt disturbance less visible when the helicopter was below the position of the goats during ground surveys.

The availability of overhead shelters appeared to affect the degree of overt disturbance response exhibited by mountain goats. We noted a lower level of overt disturbance reaction when overhead shelters such as rock ledges, caves, or low-hanging coniferous boughs were immediately available and accessible to goats. Goats responded to the helicopter most strongly when overhead cover was not available and they were caught in the open.

We did not find lower stress reactions in mountain goat herds subjected to regular aircraft flights. In fact, we observed dramatic disturbance reactions while surveying herds with regular air traffic in the vicinity of their winter ranges. The degree to which goats can become habituated to human/aerial disturbance has not been well studied. However, our inventory flights suggest that habituation to helicopter disturbance has not occurred in our study area. As physiological stress cannot be measured during a brief helicopter survey, assumptions regarding habituation must be made with caution. The sample size of herds in close proximity to heavily used flight paths is limited; further work is required to assess the degree to which habituation may occur based on overt responses. Other factors such as distance, relative elevation, availability of security shelters, and weather conditions must be considered (Frid 1997). Distances of up to 2 km have been suggested as the distance at which behavioural changes are evident in response to helicopters (Côté 1996). The threshold distance at which goats exhibit overt disturbance behaviour has not been determined by this study. We hope to conduct further analysis of the video data to assess this factor.

MANAGEMENT IMPLICATIONS

The implications of mountain goat sensitivity to helicopter disturbance for timber harvesting operations are significant. The disturbance levels presented in Figures 2 and 3 are based on mountain goat overt disturbance responses to a Bell 206-B helicopter and a total exposure time of less than 1 minute. The large heavy-lift helicopters used for commercial timber harvesting and the sustained noise of cedar shake salvaging are far more disruptive than a brief survey with a Bell 206. There is a valid concern than sustained industrial helicopter activity can negatively affect mountain goats if repeated flight paths occur over or adjacent to occupied habitats. The use of industrial helicopters in close proximity to winter range habitats for forest harvesting is expected to have chronic detrimental affects on mountain goat populations. The increased use of helicopters for winter recreation is also of concern where flight paths cross winter range habitats. For these reasons, the Lower Mainland Region of the Ministry of Environment has implemented a timing policy restricting industrial operations adjacent to mountain goat winter range habitat (Appendix 1). Our findings support the implementation of measures to reduce helicopter activity near occupied mountain goat habitat during the winter months. Timing restrictions and mitigation measures for industrial activities adjacent to ungulate winter ranges must be implemented to ensure disturbance levels are minimized and alienation of mountain goats from otherwise viable habitats does not occur (Appendix 1).

We intend to further compare group size, use of aspect, elevation and slope classes using sighting data and composition of identified winter range habitat polygons between the 3 Lower Mainland Districts of the British Columbia Ministry of Environment, Lands and Parks. We also intend to review sighting data according to ecosystem type to compare winter habitat use between coastal and interior mountain goat ecotypes. To date, the degree of coastal goat association with forest cover has been assessed through review of the video data subset only. Ongoing review of all sightings via air photo and forest cover mapping will assess the degree of forest cover association for the entire data set of 716 mountain goat sightings. We also hope to review the degree of mountain goat use of forested stands in winter through compilation and analysis of all track sightings. Further work is required to assess the level of reaction to helicopter presence compared to group composition (nursery vs. bachelor groups). More restrictive management of helicopter/industrial activities may be required adjacent to areas occupied by nursery groups to reduce potential long-term impacts of disturbance on mountain goat populations and habitat use.

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Appendix 1.

July 15, 1997

BC Environment Region 2 Mountain Goat Winter Range Timing Restriction Policy

Background:

Mountain Goats (*Oreamnos americanus*) are a species of management concern in the Lower Mainland Region and have been shown to be extremely sensitive to human-induced disturbance. Due to their sensitivity to disturbance, special measures are necessary to ensure mountain goats are not adversely affected by proposed industrial operations. Of particular concern is activities proposed in close proximity to areas utilised by mountain goat populations as winter range habitat. Such areas often provide critical escape terrain, security and thermal cover, and foraging opportunities for goats during the winter months. Disturbance during critical periods may discourage mountain goats from travelling to suitable winter range habitats, forcing them to occupy sub-optimal habitats thereby reducing their chances of survival, or displace them completely. To ensure protection of over wintering mountain goats, BC Environment requires that all activities within 500 metres of winter range habitat be restricted to the period of May 1 to October 31 in a given year. BC Environment, Fish and Wildlife Management has developed the following policy regarding all proposed industrial activities adjacent to winter range habitats outside this timing window:

1. All industrial operations within 500 metres of known mountain goat winter range habitat must be undertaken between May 1 to October 31 in a given year. Deviations or extensions to this timing window will not normally be granted except as outlined below. Note: 500 metres is considered a minimum distance based on the results of reviews of existing literature and field observations of mountain goat behaviour by Fish and Wildlife Management staff. There may be occasions where operations greater than 500 metres from winter range habitats may require application of a timing restriction due to site specific factors such as elevation, aspect, topography, heavy snowfall, etc. An additional timing restriction may be applied after May 1 where critical natal habitats are identified by Fish and Wildlife Management.
2. Extension requests will not be considered after November 15 or before April 15. Any extensions granted will be on a day to day basis, dependent upon weather conditions and presence of goats. Works areas are to be kept small so operations can be stopped on short notice.
3. Extensions will not be granted for activities involving significant or sustained disturbance such as helicopter yarding, road construction with heavy equipment, drilling, or blasting.
4. Each extension request will be evaluated on its own merit according to the historical intensity of mountain goat use of an area, type of work proposed, current weather conditions and short and long term weather forecasts. Note that any relaxation of operational constraints is contingent upon goats not using the area and continuation of

favourable weather conditions.

5. The absence of mountain goats must be determined prior to operations outside the constrained work period. It is the proponent's responsibility to conduct a brief aerial survey (to the satisfaction of Fish and Wildlife Management staff) to confirm that goats are not present. If any sign of mountain goat activity is noted within 500 metres of the proposed operational area, all work must cease and no extension will be granted. Note that helicopter flights in themselves can cause excessive disturbance to wintering goats. If goats or tracks are sighted during overflights, the flight should be terminated immediately and the location and type of sign forwarded to F&W staff. **Repeated overflights of occupied habitats are not to occur.**
6. Fish and Wildlife Management staff must be informed in writing of the results of assessments prior to work occurring. Reports will then be assessed by this agency to determine if relaxation of the work window is appropriate. Works outside the timing window are not permitted until confirmed by Fish and Wildlife Management staff.
7. When an extension has been granted, work may be allowed to continue when minor snowfalls (i.e. less than 8 hours duration and less than 0.3 metres in depth) occur. However, when snowfalls exceed 0.3 metres in depth or continue for longer than 8 hours, all work is to cease and the timing restriction will be enforced.
8. Fish and Wildlife Management may revise this protocol subsequent to receipt of additional information.
9. Where the locations of known mountain goat winter ranges have been provided to the licensee, it must be shown on operational Plans (i.e. Forest Development Plans) to reflect "best known information" as per Section 11 of the Operational Planning Regulations.
10. Fish and Wildlife Management reserves the right to recommend non-approval of extension requests where proposed works present an unacceptable risk to over-wintering mountain goat populations.

Please be advised that BC Environment will be updating winter range maps once the results of the 1997/98 FRBC mountain goat winter range inventory have been collated.

Please contact the appropriate BC Environment, Fish and Wildlife Management District staff (Forest Ecosystem Specialists or Habitat Protection Officers) in your area if you have any questions or require further information.

Brian Clark
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Fish and Wildlife Management
BC Environment
Lower Mainland Region

Biennial Symposium Northern Wild Sheep and Goat Council 12:38.

AN EVALUATION OF A GIS-BASED HABITAT MODEL FOR BIGHORN SHEEP WINTER RANGE IN GLACIER NATIONAL PARK, MONTANA

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Abstract: Increasing interest in restoring bighorn sheep (*Ovis canadensis*) populations through reintroduction and augmentation has led wildlife managers to pursue Geographic Information System (GIS) software programs as a means to quantitatively assess large land areas for suitable bighorn sheep habitat. A distinct need, however, exists for performance tests of GIS-based predictions of bighorn sheep presence or absence, and assessments of potential reintroduction sites. Recently, a National Park Service (NPS) bighorn sheep restoration program used a GIS-based Habitat Evaluation Procedure (HEP) to identify suitable habitat for reintroductions in Rocky Mountain Region National Parks and adjacent lands. In Montana's Glacier National Park, systematic ground surveys for bighorn sheep on winter ranges provide for a rigorous test of the winter range habitat component of the HEP being used by the NPS restoration program.

The GIS-based HEP delineates suitable habitat through user-defined criteria for basic habitat parameters: escape terrain (slope), escape terrain buffer, aspect, water sources, natural barriers, man-made barriers, and human development. GIS-based delineations are derived from USGS digital elevation models, digital line graphs, and digitized features from topographic maps. The HEP may also incorporate, either from GIS databases or from field-gathered data, information on vegetation composition, horizontal visibility (vegetation height and density), and presence of domestic livestock.

Through identification of the parameters that best explain observed bighorn sheep locations on Glacier National Park's two primary winter range areas, the accuracy of suitable winter range habitat predictions generated by the GIS-based HEP will be assessed. Bighorn sheep surveys, conducted during January through April of 2000 and 2001, are augmented with focal observations of individual sheep during daylight hours for 2 or 3 consecutive days to guard against under-representation of sheep use in some habitat types.

Preliminary results from ground surveys in January and February 2000 indicate that ewe-lamb bands primarily use high-elevation (6800-7600 feet) ridges and saddles characterized by broad scree and talus slopes and sparsely distributed alpine vegetation; while ram groups primarily use mid-elevation (5600-6400 feet), south-facing slopes with patchy fescue grasslands. Two significant management concerns for Glacier National Park are poaching of bighorn sheep and trespass of livestock within Park boundaries. Modeling of bighorn sheep winter range will allow assessment of Park boundary areas where sheep may be excluded from suitable winter range.

Biennial Symposium Northern Wild Sheep and Goat Council 12:39.

GPS WILDLIFE COLLARS: BIAS FROM TOPOGRAPHICAL AND COASTAL FOREST CANOPY CONSTRAINTS

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Abstract: GPS wildlife collars have proven valuable research tools under many conditions. However, studies conducted within steep, narrow and heavily-forested coastal valleys are limited. I am currently conducting a mountain goat winter habitat study in coastal British Columbia near Knight Inlet using GPS collars (Lotek 2000L model). I plan on taking the following measures of collar performance: proportion of successful fixes, proportion of 2 dimensional vs. 3 dimensional fixes, and the levels of Dilution of Precision (DOP). Increasing the proportion of 3D fixes is desirable because it allows for a new elevation to be calculated with each fix (Moen *et al*. 1997), and when DOP is low, the spread of contributing satellite signals becomes wider, thereby improving satellite configuration geometry and increasing accuracy (Rempel *et al.* 1995). However, an evaluation of GPS performance based solely on the data I obtain from these animals may be biased because I can only determine location presence and not absence; forest canopy has been shown to have a negative effect on GPS satellite reception (Rempel and Rodgers 1997 and Moen *et al*. 1996), and the rugged topograpny of B.C.'s Coast Mountains places added constraints on collar performance. Therefore, I placed 3 additional GPS collars within forested habitats selected from 3 valleys of similar biogeoclimatic classification to the primary goat study site. Valleys of varying relief were selected to address the important GPS wildlife collar issue of topography. Categories of forest habitat included 3 tree height ranges, 2 canopy closure types and 3 ranges of topographical access to satellites. GPS collars were programmed to take repeated locations at 30 minute intervals from each sample location over a 24-hour period and the proportion of successful fixes (2D and 3D fixes) was recorded. The specific effects of topographic and forest habitat variables on GPS fix success were evaluated. Observations from this ground testing and from the collared mountain goats should allow me to address the suitability of GPS wildlife collars for species that inhabit the forests and topographical relief typical of British Columbia's coast.

Biennial Symposium Northern Wild Sheep and Goat Council 12:40-53.

PNEUMONIA AS A CAUSE OF MORTALITY IN TWO DALL'S SHEEP IN THE MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES, CANADA

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Abstract: Fresh, intact carcasses of 2 adult Dall's sheep (*Ovis dalli dalli*) ewes were recovered from the northern Mackenzie Mountains, Northwest Territories on 11 June and 25 July 1999. Both ewes were emaciated and post mortem examinations demonstrated severe, subacute to chronic, fibrino-purulent bronchopneumonia, with bacterial septicaemia in the first ewe. Gross and histological lesions along the dorso-caudal borders of the diaphragmatic lobes of both ewes were consistent with the lungworm *Protostrongylus stilesi*. Eggs consistent with those of *Parelaphostrongylus odocoilei* (muscleworm) were observed in lung histological sections of the first ewe. Bacterial culture of lung and other tissues from the first ewe yielded a pure growth of *Arcanobacterium* ("*Actinomyces*") *pyogenes*, and from the second ewe, a mixed population including *Escherichia coli*, *A. pyogenes*, and, from lung tissue only, a *Mannheimia* ("*Pasteurella*") species. Bacterial cultures of lung tissue collected previously from 6 healthy ewes from the same region yielded only an unusual *Corynebacterium* species. Fixed lung and tracheal tissues from both ewes that were found dead were examined by immunohistochemistry for *Mycobacteria* spp., *Haemophilus somnus*, and *Mannheimia haemolytica*; the bovine respiratory viruses parainfluenza type 3, bovine herpes type 1, and bovine respiratory syncytial virus; and bovine viral diarrhea. The second ewe was positive for *Mycobacterium* sp.; all other samples were negative. Fecal parasitology revealed coccidia and *Trichuris* in the first ewe, *Protostrongylus* sp. larvae in the second ewe, and, in both ewes, the gastrointestinal trichostrongyles *Marshallagia* and *Nematodirus*. These are the first confirmed reports of pneumonia as a primary cause of mortality in Dall's sheep. In addition to these 2 cases, in September 1999, we received reports of 2 rams with signs of respiratory distress and 3 dead adults (2 rams, 1 ewe) from 2 different sites in the northern Mackenzie Mountains. One of the ill rams was shot and culture of lung tissue was positive for *A. pyogenes*. The significance of these mortalities in Dall's sheep demographics in the Mackenzie Mountains is unknown. In light of the importance of pneumonia as a mortality factor in bighorn sheep (*Ovis canadensis*), we, in cooperation with outfitters and hunters, have begun a project to monitor and further investigate the health status of Dall's sheep in the Mackenzie Mountains.

The Mackenzie Mountains of the western Northwest Territories are inhabited by an estimated 14,000-26,000 Dall's sheep (*Ovis dalli dalli*) (Veitch et al. 2000). This population is relatively stable, and major mortality events ("die-offs") observed in bighorn sheep (*Ovis canadensis*) have never been reported in this population (Simmons et al. 1984; Veitch and Simmons 1999) or in Dall's sheep elsewhere in their range (Bowyer and Leslie 1992; Nichols and Bunnell 1999). Conversely, the stress-lungworm-pneumonia complex in bighorn sheep is the most important cause of mortality in some bighorn populations (Forrester 1971; Aguirre and Starkey 1994; Bunch et al. 1999).

In 1997, a parasitological investigation was initiated to determine if *Umingmakstrongylus pallikuukensis*, a lungworm of muskoxen (Hoberg et al. 1995) was present in Dall's sheep of the Mackenzie Mountains. *Umingmakstrongylus pallikuukensis* was not found, but 2 other protostrongylids were identified, *Protostrongylus stilesi*, the lungworm of bighorn sheep, and *Parelaphostrongylus odocoilei*, a muscleworm which had not previously been reported in wild sheep (Kutz et al. 2001). Both parasites are common and widespread in the Mackenzie Mountain sheep population, and have the potential to cause significant pulmonary damage (Kutz et al. 2001).

In 1999, the Thinhorn Health Investigation Network (THIN) launched the Dall's sheep Health and Parasitology Project to investigate the role of these protostrongylids and other potential pathogens in the health of Dall's sheep. This project includes passive surveillance and opportunistic carcass collection. This report summarizes our findings in 1999; monitoring will continue in 2000 and 2001. While on one occasion a carcass was discovered by the investigators and a field necropsy performed on site, the only people routinely present in sheep range within the Mackenzie Mountains are outfitters; guides; non-resident, resident, and subsistence hunters; and staff from the Department of Resources, Wildlife, and Economic Development.

METHODS

In total, 5 dead and 2 sick sheep from the northern Mackenzie Mountains, NT, were reported in 1999. We examined a small lung sample from 1 sick ram that was shot (Ram 1) and necropsied 2 of the 5 dead sheep (Ewe 1 and 2). Three samples were taken from most tissues, 1 fresh, 1 frozen, and 1 preserved in 10% neutral buffered formalin. Fixed tissues were sectioned, mounted in paraffin, and stained with hematoxylin and eosin for histology. Femurs were frozen and later marrows were collected to determine percent fat content.

Tissues were cultured on MacConkey's and blood agar. Fresh samples from Ewe 1 were refrigerated and cultured 4 days later, and paired frozen samples were cultured 3 months later. The carcass of Ewe 2 was kept cool for 48 hours, and fresh samples were then cultured. The lung sample from Ram 1 was kept frozen for 1 week, and cultured immediately upon thawing.

Fixed lung and tracheal tissues from both ewes were stained immunohistochemically for: infectious bovine rhinotracheitis virus (IBR), parainfluenza-3 virus (PI_3), bovine respiratory syncytial virus (BRSV), bovine viral diarrhea virus (BVD), *Mycobacteria spp.*, *Haemophilus somnus*, and *Mannheimia haemolytica* (Haines and Chelack 1991).

Right ears (previously frozen) of both ewes were curetted, and the scrapings placed in 10% KOH for 10 min in a boiling water bath. This mixture was centrifuged for 10 minutes, decanted, and the sediment resuspended in sugar solution. This was centrifuged again for 10 minutes with a cover slip on top of the test tube, which was removed, placed on a slide, and examined for ectoparasites.

The mucosal surface of the abomasa of each ewe was rinsed and lightly scrubbed 3 times with tap water. The rinse was collected and contents brought to 1 L final volume. Two 10% aliquots were fixed in 10% neutral buffered formalin. The remaining contents were preserved in 37% formalin. In Ewe 2, small intestinal and large intestinal/caecal contents were also retained, and abomasal nematodes were frozen in saline at -80°C for molecular work.

Fecal samples from both ewes were examined by Wisconsin quantitative flotation (Cox and Todd 1962) and a beaker Baermann larval sedimentation (Forrester and Lankester 1997). In Ewe 2, a lung wash was also performed. Five pieces of randomly selected lung tissue (from affected and unaffected areas) were placed in a plastic bag, and swirled in tap water for 1 minute. Sediment was examined in small glass Petri dishes at 25X on a dissecting scope. One hundred larvae were identified on a compound light microscope.

The remainder of the eviscerated carcass of Ewe 2 was skinned and selected skeletal muscle groups examined. The muscles of the right hind leg, right foreleg, right chest wall, left trapezius, and both longissimus dorsi were sectioned in 0.5 cm slices; muscles of the left hind proximal to the stifle and left fore proximal to the cubital joint were briefly examined. Linear hemorrhages were excised, placed in saline, then either dissected under 6.7X on a dissecting microscope or placed in a compressorium and examined under the microscope.

RESULTS

The first carcass (Ewe 1) was found during a census on 11 June 1999 at 65°03' N and 127°41' W. The second carcass (Ewe 2) was found with a live lamb in an abandoned building on the Canol Heritage Trail at 64°20' N and 128°00' W by an outfitter on 25 July 1999. On 1 September 1999, another outfitter reported 2 sick rams at 64°20' N and 129°30' W that had coughs and nasal discharges, and were ostracized by nearby healthy rams. One of the sick rams (11.5-years-old) was harvested (Ram 1) and a small lung sample containing an abscess was examined. In another northern outfitting zone in early September, 3 adult sheep were found dead with no sign of predation; these carcasses were not recovered. In total, five mortalities and 2 sick animals were reported in 1999 (Fig.1).

Gross pathology

In Ewe 1, little autolysis was present, the carcass was moderately dehydrated, and the estimated time elapsed since death was 2-6 hours. Age as determined by horn annuli was approximately 10 years, and the ewe was lactating. The animal had no back, renal, or omental fat, and the femoral marrow fat content was 45%. There was a bloody discharge from the left nostril and the vulva. Ecchymotic hemorrhages were present on conjunctiva, vulvar mucosa, subcutaneous and intradermal tissues, and rumen serosa.

The most significant findings were in the thoracic cavity. There was approximately 500 ml of free serosanguinous fluid. On the right side, the visceral pleura of the cranial and accessory lobes were adhered (both fibrinous and fibrous adhesions) to the thickened parietal pericardium and to the costal pleura. On the left, a thick fibrinous/fibrous sheet, extending from the

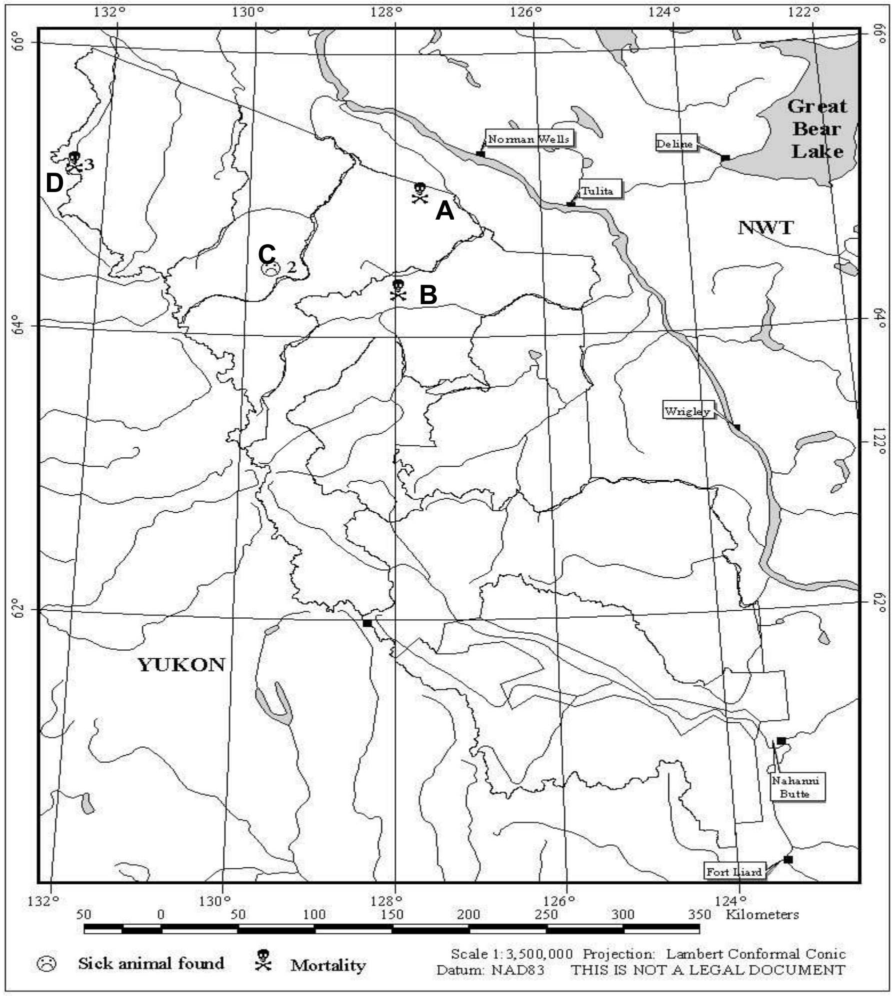

Figure 1: locations of known sick and dead Dall's sheep in the Mackenzie Mountains, Northwest Territories, June-September 1999. Numbers refer to the number of sick or dead animals at the site, while letters correspond to the animal in the text of the paper (Ewe 1 = A, Ewe 2 = B, Ram 1 = C, anecdotal report of 3 dead adults = D).

a cranial border of the cranial lobe to the middle of the diaphragmatic lobe, was dhered to the cranio-ventral costal pleura, displacing the cranial lobe ventrally and medially. Multifocal, coalescing foci of purulent material, ranging from liquid to caseous, were seen on the surface and upon cut section of both cranial lung lobes. The parenchyma at the dorso-caudal margins of both diaphragmatic lobes had lesions consistent with those described for *P. stilesi* by Spraker et al. (1984) and Kutz et al. (2001). There were multifocal petechial and ecchymotic hemorrhages throughout the epicardium of the heart, and a large hemorrhage ran along the paraconal interventricular branch of the left coronary artery.

The carcass of Ewe 2 was at least 48-hours-old at time of necropsy in Saskatoon. Age as estimated by horn annuli was 8 years, and the carcass weighed 34.4 kg, with a length of 146 cm and girth 93 cm. The ewe was in poor body condition, with no back, renal, or omental fat, and the femoral marrow fat content was 51%. The ewe was lactating.

The most significant findings were severe pneumonia and pleuritis, affecting approximately 75% of the left lung surface and 25% of the right. The visceral pleura of the right and left cranial lobes were adhered to the parietal pericardium. The visceral pleura of the right cranial and accessory lobes were adhered to the costal pleura, and that of the accessory and left diaphragmatic lobes to the diaphragmatic pleura. The visceral pleura of the left diaphragmatic lobe was also adhered to the parietal pericardium and to the costal pleura. Both cranial lobes and the cranio-ventral half of the left diaphragmatic lobe were completely consolidated, dark red to grey in colour, and had multiple, 2-30 mm in diameter, purulent foci on both surface and cut section. Contents ranged from liquid to caseous and, in some cases, had been replaced by an organized, pale, firm, spongy material that was well demarcated from surrounding lung tissue. The right middle and diaphragmatic lobes were voluminous and non-collapsing, and the caudo-dorsal border of the right diaphragmatic lobe contained lesions characteristic of *P. stilesi*.

The ventrum of the right mandible bore a 6x2 cm bony malformation rostral to the junction of ramus and body, associated with the impacted second molar of the right mandible. The first cheek teeth (the second premolars) of both mandibles were absent, and all cheek teeth had sharp projections on the lingual surface. The maxillary arrays of cheek teeth were complete, and the buccal surfaces had sharp projections.

Histopathology (Ewe 1 and 2 only)

In the cranial lung lobes, many bronchioles were obliterated by accumulations of degenerate neutrophils, while less affected bronchioles displayed epithelial hyperplasia and sub-epithelial mononuclear cell infiltrations. In Ewe 2, some bronchiolar borders were maintained and the neutrophils were less degenerate. There were massive quantities of fibrin and fluid in the alveoli, particularly in Ewe 1. Most blood vessels were congested, with some evidence of focal hemorrhage, and a few had marginating leukocytes. In both ewes, but more notably in Ewe 1, there were many “micro-” and “macro-abscesses” (ranging from the size of a small bronchiole to several centimeters in diameter) with necrotic centers and bacterial clumps. In Ewe 1, there were on average 4 protostrongylid eggs and/or larvae per field at 100X magnification (primarily eggs). Most of the eggs were consistent with those of *P. odocoilei* (Kutz et al. 2001), and were accompanied by mild granulomatous inflammation. Fewer eggs and larvae were present in lung sections from Ewe 2 (mean of 1.2 eggs/larvae – primarily larvae - per field at 100X magnification), and no *P. odocoilei* type eggs were observed.

Lung tissue in the caudal lobes of both ewes was generally less affected by the bronchopneumonia, although there was some congestion and hemorrhage. The alveoli in these sections were distended with air and many had ruptured. There were many nematode adults, larvae, and eggs typical of *P. stilesi*, and these were often associated with mononuclear inflammatory cell infiltrates in the alveolar interstitia. Larvae and mucous were frequently observed in the bronchioles, and, in Ewe 2, cross-sections of adult nematodes were present within bronchioles.

In the spleen of Ewe 1, there was evidence of moderate lymphocytolysis, severe congestion, and large numbers of macrophages, lymphocytes, and plasma cells in the interstitium. Ewe 1 also had mild, chronic lymphocytic/plasmacytic nephritis and granulomatous periacinar hepatitis; in Ewe 2 there was mild periacinar hepatic fibrosis. In both ewes there was renal and hepatic congestion, and numerous *Sarcocystis* spp. tissue cysts were present in both cardiac and skeletal muscle; in the cardiac muscle, these were occasionally associated with fibrosis. The pericardium of Ewe 2 was thickened and mononuclear cell infiltrations were visible in places. In Ewe 1, but not Ewe 2, there were locally extensive hemorrhages running parallel to the muscle fibers, fiber necrosis, and sarcocysts, but no muscle nematodes were observed.

Morphological diagnoses included subacute to chronic and on-going fibrinopurulent bronchopneumonia involving approximately 60% (Ewe 1) and 50% (Ewe 2) of the entire surface area of the lung, as well as fibrinous and fibrous pleuritis and pericarditis. Both ewes had moderately severe, granulomatous, verminous pneumonia in the caudo-dorsal diaphragmatic lobes. The first ewe had lesions of septicaemia, while the second had chronic right mandibular osteomyelitis ("lumpy jaw") associated with an impacted second molar.

Bacteriology (Table 1)

There was pure growth of *Arcanobacterium pyogenes* from spleen, liver, kidney, and cranial and caudal lung lobes in fresh and frozen samples from Ewe 1. Frozen pericardial and pleural fluid also yielded *A. pyogenes*. In Ewe 2, *A. pyogenes* was cultured from liver, bone marrow, and

Table 1: Results of microbiological investigation – parasitology, bacteriology, and virology – of 3 Dall's sheep of the Mackenzie Mountains, NT.

	Protostrongylid larvae	**Other parasites** (eggs or oocysts per gram of feces)	**Bacteria** Culture & immunohistochemistry (IHC)[4]	**Virology** IHC[5]
Ewe 1	*Protostrongylus*[1] (gross and histology) and *Parelapho-strongylus odocoilei* eggs (histology)	*Marshallagia* sp. (11.8) *Nematodirus* sp. (1.4) *Trichuris* sp. (4.6) *Eimeria*[3] spp. (0.4) *Sarcocystis* sp. present No ectoparasites	*Arcanobacterium pyogenes* (culture of cranial and caudal lung, other organs, pericardial and pleural fluids)	Negative
Ewe 2	Only *Protostrongylus* (gross & histology, lung wash, and 1.2 LPG Baermann)	*Marshallagia* sp. (0.6) *Nematodirus* sp. (2.0) *Sarcocystis* sp. present No ectoparasites	*A. pyogenes* (culture of cranial and caudal lung, bone marrow, and liver); *Mannheimia* sp. (culture of cranial lung); *Mycobacterium* spp. (IHC)	Negative
Ram 1	Only DSL[2] recovered on lung wash of small sample	NA	*A. pyogenes* from small lung sample; IHC NA	NA

[1] most likely *Protostrongylus stilesi* (no adult *P. rushi* observed in airways)
[2] dorsal-spined first-stage larvae, most likely *Parelaphostrongylus odocoilei* in this population
[3] most likely *Eimeria dalli, E. ahsata*, and/or *E. crandaillis* – Clark and Colwell (1974)
[4] immunohistochemistry was performed for the following bacterial antigens: *Mycobacteria* spp., *Haemophilus somnus*, and *Mannheimia haemolytica*
[5] immunohistochemistry was performed for the following viral antigens: infectious bovine rhinotracheitis virus (IBR), parainfluenza-3 virus (PI3), bovine respiratory syncytial virus (BRSV), bovine viral diarrhea virus (BVD)

cranial and caudal lung lobes (but not kidney or adrenal gland). In addition, a *Mannheimia* sp. was cultured from the cranial lung lobes of Ewe 2 only; based on standard biochemical testing this organism was characterized as *Mannheimia haemolytica*-like. Only *A. pyogenes* was cultured from the lung sample from the Ram 1.

Immunohistochemistry (Table 1)

Ewe 2 was positive for *Mycobacteria* spp. (most likely *M. avium* although this was not confirmed). All other results were negative.

Parasitology (Table 1)

Ectoparasites were not recovered from either of the ewes. Based on fecal flotation, eggs of *Marshallagia* spp. and *Nematodirus* spp. were present in both ewes; *Trichuris* spp. and *Eimeria* spp. were only present in Ewe 1. Ewe 2 was positive for *Protostrongylus* spp. larvae, but no other protostrongylid species, on Baermann and lung wash. A few dorsal-spined larvae were recovered from the lung wash of Ram 1.

DISCUSSION

These are the first reported cases of pneumonia as a cause of mortality in wild Dall's sheep. While there is little published information about pneumonia and associated pathogens in Dall's sheep, the bighorn sheep pneumonia complex has been the focus of considerable research efforts. Therefore, our results are interpreted in the context of bighorn sheep pneumonia, a disease multifactorial in origin, often involving bacteria, parasites including *Protostrongylus* spp. lungworms, viruses, and a stress 'trigger'.

Pathology

The pathological picture of subacute to chronic fibrinopurulent bronchopneumonia, fibrinous pleuritis, and pulmonary abscessation seen in the 2 Dall's ewes found dead in 1999 is very similar to that reported in pneumonia in bighorn sheep (Spraker et al. 1984; Bunch et al. 1999). Pathological lesions associated with *Mannheimia haemolytica* in most animal species are generally more fibrinous than purulent, while hallmarks of *A. pyogenes* invasion include abundant purulent material in the bronchioles and abscessation (Schwantje 1988); both processes were present in the 2 Dall's ewes examined. Granulomatous inflammation associated with lungworm lesions in the caudo-dorsal lobes and eggs/larvae in the cranial lobes was consistent with that reported for *Protostrongylus* sp. in bighorn sheep (Spraker 1979; Spraker et al. 1984; Schwantje 1986), *Muellerius* sp. in bighorn sheep (Demartini and Davies 1977), and eggs and larvae of *Parelaphostrongylus odocoilei* in Dall's sheep of the Mackenzie Mountains (Kutz et al. 2001) and mule deer (Platt and Samuel 1978; Pybus and Samuel 1984a; Pybus and Samuel 1984b). The dental abnormalities and mandibular osteomyelitis in Ewe 2 were consistent with other descriptions of lumpy jaw in wild sheep (Glaze et al. 1982; Kutny and Stenhouse 1991; Hoefs and Bunch 2001); apparently lumpy jaw is more prevalent in thinhorn sheep than in bighorn sheep (Hoefs and Bunch 2001).

Bacteria

Pneumonia in bighorn sheep most commonly involves the bacterial species *Mannheimia* (*Pasteurella) haemolytica* (various biotypes) or *Pasteurella multocida,* often in conjunction with *Arcanobacterium (Actinomyces* or *Corynebacterium)* *pyogenes* (Spraker et al. 1984; Schwantje 1988; Bunch et al. 1999). *Pasteurella/Mannheimia* spp. and *A. pyogenes* are commensals of the upper respiratory tract, tonsils, and skin (the last *A. pyogenes* only) of healthy domestic and bighorn sheep. These bacteria are opportunistic pathogens in the lungs when natural defenses are compromised by stressors or other pathogens (Queen et al. 1994; Brogden et al. 1998). One exception to this opportunistic role occurs when naïve bighorns are exposed to a foreign *Mannheimia* species from domestic sheep or biotypes from other bighorn sheep. In such instances, these bacteria may act as primary pathogens (no need for pre-disposing factors) in the naïve bighorns (Foreyt and Jessup 1982; Foreyt et al. 1994). The latter scenario is unlikely in Dall's sheep in the Northwest Territories, since there are no domestic sheep or goats within 50 km of sheep range in the Territory, nor have wild sheep or goat translocations occurred (Veitch 1996). Experimental infections of Dall's sheep have, however, illustrated that they are as susceptible to domestic animal bacteria as bighorns. In fact, *in vitro* studies show that Dall's sheep neutrophils may be more sensitive to cytotoxins of *Mannheimia haemolytica* biotype A serotype 2 (a domestic sheep strain) than neutrophils of bighorns (Foreyt et al. 1996).

We recovered *A. pyogenes* from all lung samples (Ram 1, Ewes 1 and 2) and some organs sampled in Ewes 1 and 2. An unusual *Mannheimia* sp. was isolated from the cranial lung of only 1 of the 3 Dall's sheep sampled (Ewe 2); this may, however, simply reflect the fragility of *Mannheimia* species. The positive result for *Mannheimia* sp. was from the only samples that had not been frozen or in transit for extended periods of time. Alternatively, *A. pyogenes* might have been the only bacterial species involved in the pneumonia/septicaemia, although *A. pyogenes* is more commonly found with concomitant *Pasteurella* or *Mannheimia* spp. in cases of bighorn sheep pneumonia (Marsh 1938; Buechner 1960; Demartini and Davies 1977; Spraker 1979; Foreyt and Jessup 1982).

Arcanobacterium pyogenes is likely part of the normal pharyngeal fauna of Dall's sheep. Recently, we recovered *A. pyogenes*-like bacteria from the tonsils of a healthy Dall's ewe (Jenkins and Chirino-Trejo, unpublished data), and *A. pyogenes* is the most frequently cultured bacteria from lumpy jaw in Dall's sheep (Neiland 1972; Glaze et al. 1982; Heimer et al. 1982). We have not recovered *A. pyogenes* or *Mannheimia* spp. bacteria from the lungs of any hunter-killed or collected healthy sheep, only an unusual *Corynebacterium* sp. (Kutz, Jenkins, and Chirino-Trejo, unpublished data); therefore, the presence of these bacteria in pneumonic lungs must be considered significant.

It is not surprising that the *Mannheimia* species recovered from Mackenzie Mountain Dall's sheep was distinct from those of bighorn or domestic sheep, as this Dall's sheep population has historically been isolated (Veitch and Simmons 1999) such that divergent evolution may have occurred. Further work has been undertaken to genetically characterize the *Mannheimia* sp., which was sufficiently distinct from *Mannheimia haemolytica* that the immunohistochemistry for this pathogen was negative. Immunohistochemistry was also performed for *Mycobacteria* spp. and *Haemophilus somnus*. The second ewe was positive for *Mycobacteria* sp. antigen, but due to lack of contact with humans and cattle, it was most likely *M . avium* rather than *M. bovis* or *M. tuberculosis*.

Parasites

The roles of the protostrongylid lungworms *Protostrongylus stilesi* and *Protostrongylus rushi* in the bighorn sheep pneumonia complex have been a source of controversy. Some feel that these lungworms may not play an immediate role in all-age die-offs but may instead act as a predisposing factor to fatal pneumonia (Samson et al. 1987). In the Mackenzie Mountains, wildlife biologist N. Simmons reported lesions of verminous pneumonia in harvested animals as long ago as 1967 (Simmons, Veitch, and Kutz, unpublished data), and more recent work suggests that *P. stilesi* is endemic in Dall's sheep of the Mackenzie Mountains (Kutz et al. 2001). *Protostrongylus rushi* has been recovered only from 1 Dall's sheep in the Yukon Territory (Kutz et al. 2001).

Parelaphostrongylus odocoilei has only recently been recognized in the Mackenzie Mountain Dall's sheep population (Kutz et al. 2001), and it may play a greater role than *P. stilesi* in pneumonia in Dall's sheep. While *P. stilesi* adults, larvae and eggs are usually localized to the caudal lobes, haematogenously delivered eggs and larvae of *P. odocoilei* create focal granulomas diffusely throughout the entire lung (Pybus and Samuel 1984a; Kutz et al. 2001).

Lungworm larvae can be aspirated into the cranial lobes (Schwantje 1988), where, in combination with *P. odocoilei* eggs and larvae, they cause inflammation. Such larvae may facilitate opportunistic bacterial invasion by obstructing airways, dispersing bacteria throughout the lungs, and/or causing immunosuppression (Demartini and Davies 1977; Spraker et al. 1984). Conversely, some feel that the nematodes or the tissues they damage may produce anti-bacterial substances (Vazquez 1975); it is possible, however, that bacteria are seldom recovered from the caudal lobes, where *P. stilesi* dwells, simply due to the cranio-ventral distribution of bacterial bronchopneumonia.

The lungworm, *Protostrongylus stilesi*, was present in both ewes, and *P. odocoilei* was likely present in Ewe 1 and Ram 1 (Table 1). It is unclear why Ewe 1, with many eggs and larvae present in lung histological sections, was negative for larvae on fecal parasitology. Fecal larval shedding may be decreased in chronically debilitated animals, although this has not been reported in the literature. On histology, these parasites were responsible for focal granulomatous inflammation, and in the cranial lobes, larvae and eggs were sometimes associated with bacterial abscesses. Therefore, these protostrongylids may have played a predisposing role in the pneumonia, but the proximate cause of death was no doubt the bacterial bronchopneumonia and septicaemia.

Gastro-intestinal parasites, adults of which have yet to be quantified, may have contributed to the poor body condition of the animals and thereby increased their susceptibility to pneumonia; 1 study on Montana bighorns suggests that gastro-intestinal parasites may act as a stress factor (Worley and Seesee 1992).

Viruses

Immunohistochemistry for bovine respiratory viruses was performed because they have been associated with bighorn pneumonia, and are thought to play a predisposing role in domestic sheep *Mannheimia haemolytica* pneumonia (Brogden et al. 1998). PI_3 virus has been recovered from captive and wild bighorn sheep dying from pneumonia in Wyoming and Colorado (Parks et al. 1972 and Spraker 1979, respectively), and nasal swabs of healthy desert bighorns (Clark et al. 1985). BRSV has also been implicated in the bighorn pneumonia complex (Spraker and

Collins 1986; Aguirre and Starkey 1994) and there are seropositive bighorn herds (Clark et al. 1985; Dunbar et al. 1985). IBR has been recovered from nasal swabs of healthy bighorn sheep (Clark et al. 1993), and some desert bighorn sheep were seropositive for this virus (Clark et al. 1985), as well as BVD. In Dall's sheep populations, only 1% of Alaskan Dall's sheep were seropositive for PI_3, but negative for IBR and BVD (Foreyt et al. 1983). The source of PI_3 for Alaskan Dall's sheep was most likely domestic sheep and goats in the Alaskan interior, which are also the likely source of contagious ecthyma in Alaskan Dall's sheep (Zarnke et al. 1983).

Both ewes were negative on immunohistochemistry for the bovine viruses, and it is unlikely that Mackenzie Mountain Dall's sheep have been exposed to any domestic cattle pathogens. We cannot completely rule out a viral component to the pneumonia, however, because immunohistochemistry for cattle viruses would probably not detect viruses specific to Dall's sheep. As well, it is conceivable that a virus present earlier in the disease process would not be detected in tissue in the terminal stages of the pneumonia. In future, when possible, we will do serological testing for viral pathogens.

Stress

Numerous stressors in bighorn sheep populations have been implicated in triggering die-offs, including overcrowding, decreased nutrition, loss of escape cover, harassment, noise, domestic animals, high snowfall, and high dust levels (Bunch et al. 1999). As well, some authors propose that loss of chase predators, which cull sheep heavily infected with lungworm, may lead to decreased sheep population quality and mass die-offs (Geist 1971; Uhazy et al. 1973). Most of the stressors present in bighorn populations are absent in the Northwest Territories, with the exception of some mineral exploration, aircraft intrusion, and light hunting pressure, and there has not been substantial attrition of predator (wolf and grizzly) populations (Poole and Graf 1985; Veitch and Simmons 1999; Veitch et al. 2000).

Both ewes were in poor body condition, and low bone marrow fat content (45% and 51%), particularly in midsummer, indicated severe nutritional stress (Mech and Delgiudice 1985). Both ewes were lactating, which may have increased energy demands. One of the consequences of reproduction in bighorn ewes is decreased resistance to parasites and pathogens (Festa-Bianchet 1989). The dental anomalies may well have contributed to the poor body condition of the second ewe by decreasing her foraging ability (Glaze et al. 1982).

The case reports described here are consistent with the classic pathological description of pneumonia in bighorn sheep. We observed a few differences in the microbiological fauna, namely an unusual *Mannheimia haemolytica*-like species that is probably specific to Dall's sheep, and a possible role for *P. odocoilei*. Mackenzie Mountain Dall's sheep harbor most of the necessary endemic microbiological ingredients for wild sheep pneumonia, including the newly recognized *P. odocoilei*, but the pattern of mortality is thus far one of sporadic, isolated cases and not a widespread, all-age die-off. This is most likely attributable to the lack of anthropogenic stressors (relative to bighorn sheep) and opportunities for transmission of domestic sheep and cattle pathogens within the Mackenzie Mountain Dall's sheep population. The current situation for Dall's sheep in the NWT may reflect that of bighorn sheep in western Canada and the United States before habitat loss, decreased suitability of available habitat, pathogen introduction, translocations, and loss of chase predators weakened these wild sheep populations. Thinhorn sheep managers and researchers in northern North America should continue to strive to keep their populations free of man-made stressors and introduced pathogens. Even so, natural stressors and global climate change may shift the equilibrium of host-pathogen relationships in Mackenzie Mountain Dall's sheep, and thus continued population health monitoring and baseline parasitological data collection in the Northwest Territories is necessary.

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BLOOD CHEMISTRY AND TRACE MINERAL REFERENCE VALUES FOR CALIFORNIA BIGHORN SHEEP IN OREGON

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Abstract: Many agencies, including the Oregon Department of Fish and Wildlife, routinely collect blood samples from animals captured during management, research, and transplant operations. Resulting blood chemistry and mineral data are often used as indices of animal health. However, in most cases data are compared to livestock standards because baseline values are not well established for most wildlife species. We report on analysis of over 400 California bighorn sheep blood samples taken from 6 populations over a 13 year period. Where repeated sampling events have occurred (n=3), we attempt to relate blood parameters to population performance. Relative value of this information as baseline for California bighorns is discussed.

Key words: blood chemistry, California bighorn sheep, *Ovis canadensis californiana*, Oregon, serum trace mineral.

Bighorn sheep (*Ovis canadensis*) are an extremely popular wildlife species in much of western North America. For many agencies, bighorn sheep programs are high profile in nature and may involve intensive management using trap and transplant operations, frequent population monitoring, and biological sampling to assess overall health of individual animals and populations.

Evaluation of blood chemistry parameters and mineral levels can be used to assess animal health (Puls 1995) and as a diagnostic tool for identifying disease in individual animals (Chin 1997). Difficulties arise, however, because limited information exists documenting normal blood chemistry values for wild species, and ranges reported for domestic breeds may not be representative of wild species' profiles (Hebert 1978). Additionally, stress, capture, nutritional variability, and captivity may alter blood chemistry profiles (Franzmann and Thorne 1970, Hebert 1978, Kock et al. 1987*a*, Kock et al. 1987*b*).

Limited information is available documenting blood chemistry profiles for wild sheep species. We found 2 reports of blood chemistry profiles for thinhorn sheep (*O. dalli dalli* and *O. d. Stonei*, Foreyt et al. 1983, Franzmann 1971*b*). For bighorn sheep, most reports describe blood chemistry profiles for Rocky Mountain bighorn sheep (*O. c. canadensis*, Bottrell et al. 1978, Davies 1976, Franzmann 1971*a*, Franzmann and Thorne 1970, Hebert 1978, Woolf and Kradel 1969) or desert bighorn sheep (*O. c. nelsoni*; Borjesson et al. 2000, McDonald et al. 1981). Only 1 report specifically decribes blood chemistry profiles for California bighorn sheep (*O. c. californiana*; Bottrell et al. 1978). Throughout all reports we found for all species or subspecies of wild sheep, data were not consistent with regard to which parameters were specifically reported and with few exceptions, sample sizes were generally limited with regard to development of normal values and ranges.

We analyzed results of over 400 blood

samples collected from 6 California bighorn sheep populations over a 13-year period. Our objectives for this analysis were:

1) To evaluate the effects of age and sex on mean serum chemistry values;
2) Compare mean serum chemistry values across time within populations with repeated sampling events;
3) Compare mean serum chemistry values between populations within sampling years where multiple populations were sampled;
4) Explore the possibility of relationships between blood chemistry and population growth; and
5) Develop normal values and reference ranges for blood chemistry of California bighorn sheep.

STUDY AREAS

California bighorn sheep were native to the fault-block mountains and high plains of southeastern Oregon but were extirpated by about 1915 (Oregon Department of Fish and Wildlife 1992). In 1954, California bighorns from British Columbia were reintroduced to Hart Mountain and since establishment have been captured and used for transplants to suitable habitat throughout most of central and southeastern Oregon. A spring 1992 population estimate indicated Oregon had about 1,950 California bighorns (Oregon Department of Fish and Wildlife 1992). By 1999, populations had increased to over 2,700 animals (Oregon Department of Fish and Wildlife 1999).

Hart Mountain is a major fault-block mountain range that has its escarpment facing west. It is within the Hart Mountain National Antelope Refuge, and reaches an upper elevation of 8,065 feet. The escarpment drops 3,600 feet to the Warner Valley at the base of the west slope. Bighorns are associated with the rugged cliffs and adjacent sagebrush ridges.

Steens Mountain also is a fault-block mountain, but its escarpment faces east. Elevation drops from 9,730 to 4,200 in about 5 lateral miles. Bighorns primarily occupy moist, green, hanging valleys and cirques carved by glaciation. Precipitous cliffs provide excellent lambing habitat. Bighorns were reintroduced to Steens Mountain in 1960 from the established population on Hart Mountain.

Leslie Gulch is a rimrock canyon associated with the rugged Owyhee River Canyon of Malheur County, Oregon. It lies east of Owyhee Reservoir and is formed by highly dissected canyons within ancient lava flows. Elevations range from about 6,000 feet on Mahogany Mountain to about 2,500 feet at the water's edge of Owyhee Reservoir. Bighorns were established in Leslie Gulch in 1965 from the Hart Mountain population.

Both the John Day River and Deschutes River herds occupy major river canyon habitats. Elevations are lower (600 – 3,000 feet) than most other Oregon California bighorn ranges. The John Day River herd was established with a 1989 release from the Hart Mountain herd and a 1990 release of British Columbia California bighorns. The Deschutes River herd was established during 1995 with a transplant from the established population on Steens Mountain. The John Day River also has received additional transplants from British Columbia and the Deschutes River.

The Santa Rosa Mountains of northern Nevada are similar to several mountain ranges of southeastern Oregon, but are not uplifted fault-block mountains. The 16 bighorns sampled in 2000 were captured on Sawtooth Mountain near Orovada, and in 8–Mile Canyon south of McDermitt. These bighorns were released onto Steens Mountain as part of a genetics research study recently initiated by Oregon. The Santa Rosa herd was originally established using bighorns from Penticton, British Columbia.

METHODS

All but 16 of 423 bighorns sampled for this study were captured using Coda Netgun technology (Barrett et al. 1982). The remaining 16 were captured using a linear drive net and a helicopter (Beasom et al. 1980). Early netgun operations utilized department personnel but captures occurring after 1990 were performed by contractors with specific experience with bighorn sheep. Contractors provided aircraft, pilots, gunners, muggers and appropriate equipment for capture and transport of bighorns to base camp. Department personnel managed base camp operations including health evaluation, veterinary care, biological sampling, vaccinations, marking (eartag, telemetry), and vehicle transport if required. A veterinarian was present for most capture operations and animal handling protocols were consistent with care and use guidelines of the American Society of Mammalogists (1987).

All blood samples were collected by a designated capture crew member or the veterinarian. A 50 ml sample was collected by jugular venipuncture from each bighorn using a 1.5 inch 16–20 gauge needle and a 60 cc syringe. Samples were immediately placed in sterile glass tubes without anticoagulant. All records and samples were cross-referenced with capture data sheets and included animal ID, age, sex, health and condition data, inoculations received, samples collected, tag and transmitter information, and pertinent comments.

Blood samples were maintained at ambient temperature (or in a warm pickup cab) for about 2-hr prior to being centrifuged for harvest of serum. Serum was decanted into cryotubes, labeled, and frozen for 1-3 weeks until capture operations were complete for a year, or until entire groups of samples could be sent in a single shipment to appropriate labs for analyses. A sub-sample (3–5 ml) was retained from each bighorn and currently is maintained frozen in a serum bank by the department.

The majority of samples for this study were analyzed by the Veterinary Diagnostic Laboratory at Oregon State University in Corvallis, Oregon. Samples collected in 1988 were analyzed at the Central Oregon Laboratory in Bend, Oregon, and those done in 1989 were analyzed at the Treasure Valley Laboratory, Inc. in Boise, Idaho. Serum was analyzed for the following parameters: blood urea nitrogen (BUN, *mg/dl*), total protein (*g/dl*), albumin (*g/dl*), globulin (*mg/dl*), creatinine (*mg/dl*), creatine kinase (CK, *IU/l*), glucose (*mg/dl*), cholesterol (*mg/dl*), total bilirubin (*mg/dl*), direct bilirubin (*mg/dl*), indirect bilirubin (*mg/dl*), gamma-glutamyltransferase (γGT, *IU/l*), lactate dehydrogenase (LDH, *IU/l*), alanine aminotransferase (ALT, *mg/l*), aspartate aminotransferase (AST, *IU/l*), sorbitol dehydrogenase (SDH, *IU/l*), uric acid (*mg/dl*), calcium (Ca, *mg/dl*), phosphorous (P, *mg/dl*), sodium (Na, *Meq/l*), chloride (Chl, *Meq/l*), potassium (K, *Meq/l*), magnesium (Mg, *mg/l*), iron (Fe, *mCg/dl*), and carbon dioxide (CO_2, *Meq/l*). Ratios of albumin:globulin, BUN:creatinine also were calculated from lab results. Abbreviations and measurement units are consistent with those reported by Puls (1995).

Individual parameter values were first compared using Analysis of Variance (AOV). Data comparing mean values between male and female sheep were compared using *t*-tests. Where 3 or more means were compared (e.g. age classes, across multiple years within a population, across multiple populations within a year) an *F*-test was used to determine if individual mean parameter values differed. Tests between individual means were conducted using Least Significant Difference (LSD) tests but were only conducted when the *F*-test was significant. All mean comparisons were considered significant when $P \leq 0.05$. The central 90th percentile was used to determine the normal range for each parameter. The median, mean ($\bar{x}$), standard error (SE), and coefficient of variation (CV) for each parameter also were determined for comparisons in this study and comparison with other reported studies. No assumption of normality was made, even though many parameter distributions approximated normality. Using 4 parameters consistently found across 12 sampling events (blood urea nitrogen [BUN], creatinine, BUN:creatinine ratio, and asparate aminotransferase [AST]) we used stepwise linear regression to determine their relationship with net population growth rate ($R_0 = N_{t+1}/N_t$).

RESULTS

Over 400 blood samples were collected from 6 distinct California bighorn sheep populations over a 13-year period (Table 1). Three populations (Hart Mountain, Steens Mountain, John Day River) had 3 or more sampling events allowing comparison within populations through time. In 3 years (1994, 1995, and 2000) 3 distinct populations were sampled allowing comparisons across populations within a year. Because most capture operations were conducted for transplant operations, females (n=314) dominated the samples where sex was identified (n=399) and adults (n=264) dominated samples where age was identified (n=367).

Few differences in mean blood chemistry parameters were found between males and females (Table 2). Of those that differed, most were generally associated with nutrition. Mean blood urea nitrogen (P = 0.001) and mean BUN:Creatinine ratio (P = 0.002) were higher for males. Mean total protein (P = 0.036), albumin (P = 0.026), and creatinine (P = 0.043) values were higher in females. Only 1 diagnostic parameter, mean total CO_2, differed between the sexes and was higher in males.

Parameters indicative of nutrition also tended to differ between age class (lamb, yearling, adult) of bighorns (Table 3). Mean values for adults and yearlings tended to be similar whereas lambs tended to differ from yearlings, or yearlings and adults. Mean blood urea nitrogen ($P < 0.01$) and BUN:Creatinine ratio (P <0.01) were higher for lambs than for either yearling or adults which did not differ from each other. Total

Table 1. Minimum sample size, sample population, and sample year for blood parameters of California bighorn sheep in Oregon, 1988-2000.

	Year								
Herd Sampled	1988	1989	1990	1994	1995	1996	1999	2000	Total
Hart Mountain		17	52	39	32	29			169
Steens Mountain	23			20	18			17	78
John Day River			13			13	20	28	74
Leslie Gulch				20	38				58
Deschutes River							28		28
Santa Rosa Mt, NV								16	16
Total	23	17	65	79	88	42	48	61	423

Age/Sex	Male	Female	Lamb	Yearling	Adult
N	85	314	47	56	264

Table 2. Mean blood serum chemistry values for male and female California bighorn sheep in Oregon, 1988-2000.

	Male		Female			
Parameter	n	$\bar{x}$	n	$\bar{x}$	*T*	*P*<|*T*|
Blood Urea Nitrogen (BUN, *mg/dl*)	85	18.5	314	15.3	-3.35	0.001
Total Protein (*g/dl*)	69	6.8	251	6.9	2.11	0.036
Albumin (*g/dl*)	69	3.8	251	4.0	2.26	0.026
Globulin (*mg/dl*)	23	2.8	86	2.7	-0.77	0.438
Albumin:Globulin Ratio	23	1.4	86	1.5	1.44	0.153
Creatinine (*mg/dl*)	64	2.0	247	2.2	2.04	0.043
BUN:Creatinine Ratio	64	10.3	246	7.7	-3.22	0.002
Creatine Kinase (*IU/l*)	41	1319	161	1031	-0.98	0.330
Glucose (*mg/dl*)	64	152	247	149	-0.46	0.577
Cholesterol (*mg/dl*)	23	58.6	86	57.2	-0.63	0.464
Total Biliruben (*mg/dl*)	48	0.2	184	0.2	0.19	0.847
Direct Biliruben (*mg/dl*)	23	0.0	86	0.0	0.01	0.996
Indirect Biliruben (*mg/dl*)	23	0.1	86	0.1	0.14	0.890
γGT[1] (*IU/l*)	56	64.3	183	56.7	-1.43	0.155
LDH[1] (*IU/l*)	29	766	131	791	0.59	0.556
ALT[1] (*mg/l*)	10	42.7	18	38.6	-0.87	0.393
AST[1] (*IU/l*)	85	277	314	234	-1.80	0.075
SDH (*IU/l*)	25	37.5	98	40.8	0.32	0.753
Uric Acid (*mg/dl*)	13	0.2	68	0.2	0.21	0.836
Calcium (*mg/dl*)	69	10.5	251	10.6	0.39	0.700
Phosphorous (*mg/dl*)	69	6.7	251	6.7	-0.16	0.877
Sodium (*Meq/l*)	69	153	251	154	1.45	0.147
Chloride (*Meq/l*)	69	97.0	251	98.1	1.15	0.254
Potassium (*Meq/l*)	69	5.0	251	5.3	1.44	0.151
Magnesium (*mg/l*)	46	3.1	165	3.2	1.14	0.257
Total Carbon Dioxide (*Meq/l*)	25	10.0	98	5.5	-2.29	0.031
Iron (*mCg/dl*)	13	209	68	199	-0.69	0.490

[1] γGT=Gamma-glutamyltransferase; LDH=Lactate dehydrogenase; ALT=Alanine aminotransferase; AST=Aspirate aminotransferase; SDH=Sorbitol dehydrogenase.

protein differed (P <0.01) across all age classes with lambs having the lowest and adults having the highest mean value. Mean globulin value was lowest in lambs and greatest in yearlings, with no difference between lambs and adults or between adults and yearlings (P = 0.01). Mean creatinine values were lowest in lambs (P < 0.01). Direct bilirubin and total CO_2 differed (P < 0.01) with direct bilirubin lower in lambs, and CO_2 higher in lambs than for yearlings and adults. Sodium and chloride were the only electrolytes that differed (P < 0.01) and tended to be lower in lambs.

Considerable variation existed across populations analyzed within years (Table 4).

Table 3. Mean serum chemistry values for lamb, yearling, and adult California bighorn sheep in Oregon, 1988-2000. Means within a row with the same letter are not different (LSD, $P = 0.05$).

	Lamb		Yearling		Adult			
Parameter	N	$\bar{x}$	n	$\bar{x}$	N	$\bar{x}$	*F*	*P>F*
BUN (*mg/dl*)	47	19.3a	56	16.1b	264	15.7b	5.33	<0.01
Σ Protein (*g/dl*)	45	6.3a	42	6.7b	201	7.0c	17.49	<0.01
Albumin (A, *g/dl*)	45	3.7	42	3.9	201	3.9	2.44	0.09
Globulin (G, *mg/dl*)	21	2.6a	8	3.1b	62	2.8ab	4.47	0.01
A:G Ratio	21	1.6	8	1.4	62	1.5	1.22	0.30
Creatinine (C, *mg/dl*)	37	1.9a	45	2.1b	197	2.2b	8.18	<0.01
BUN:C Ratio	36	11.6a	45	8.6b	197	7.9b	8.73	<0.01
Creatine Kinase (*IU/l*)	16	1769	37	890	135	1078	2.01	0.14
Glucose (*mg/dl*)	37	142	45	152	197	149	0.98	0.38
Cholesterol (*mg/dl*)	21	54.0	8	59.6	62	57.9	1.90	0.16
Σ Biliruben (*mg/dl*)	35	0.1	31	0.2	134	0.1	0.19	0.85
Dir. Biliruben (*mg/dl*)	21	0.0a	8	0.1b	62	0.0a	8.72	<0.01
Ind. Biliruben (*mg/dl*)	21	0.1	8	0.1	62	0.1	0.10	0.89
γGT[1] (*IU/l*)	32	47.9	34	66.0	159	59.4	2.32	0.10
LDH[1] (*IU/l*)	15	803	22	862	105	154	0.96	0.38
ALT[1] (*Mg/l*)	8	40.6			20	39.8	0.02	0.88
AST[1] (*IU/l*)	47	267	56	235	264	240	0.62	0.54
SDH[1] (*IU/l*)	14	33.0	23	40.0	72	34.0	0.21	0.81
Uric Acid (*mg/dl*)	13	0.2	8	0.1	42	0.2	0.86	0.43
Ca (*mg/dl*)	45	10.1	42	10.3	201	10.8	0.60	0.55
P (*mg/dl*)	45	4.8	42	5.2	201	5.2	1.64	0.20
Na (*Meq/l*)	45	149a	42	153ab	201	155b	7.07	<0.01
Chl (*Meq/l*)	45	94.5a	42	95.5a	201	99.0b	5.81	<0.01
K (*Meq/l*)	45	4.8	42	5.2	201	5.2	1.64	0.20
Mg (*mg/dl*)	24	2.9	34	3.0	139	3.2	2.66	0.07
Σ CO_2 (*Meq/l*)	14	14.4a	23	6.6b	72	5.3b	19.94	<0.01
Fe (*mCg/dl*)	13	216	8	180	42	210	2.16	0.12

[1] γGT=Gamma-glutamyltransferase; LDH=Lactate dehydrogenase; ALT=Alanine aminotransferase; AST=Aspirate aminotransferase; SDH=Sorbitol dehydrogenase.

Mean BUN values were higher ($P < 0.01$) in Leslie Gulch compared to Hart Mountain and Steens Mountain during both 1994 and 1995. Creatinine and BUN:Creatinine ratios differed across populations in 1994. Asparate aminotransferase differed ($P <$ 0.01) during 1994 but not during 1995 ($P =$ 0.66). Four minerals differed (Ca, P, Na, and Mg, $P < 0.01$) between populations during 1995. All nutritional indices analyzed except for glucose and mean total bilirubin, calcium, phosphorous, and potassium differed ($P < 0.01$) between Steens Mountain, John Day River, and Santa Rosa Mountains (Nevada) populations during 2000.

Considerable variation also existed within populations through time (Table 5).

Table 4. Mean blood serum chemistry values within years for California bighorn sheep in Oregon. Means within a row with the same letter are not different (LSD, P = 0.05).

Year Parameter	Population Hart	Steens	Leslie	F	$P>F$
1994					
BUN (*mg/dl*)	9.4a	13.9b	17.4c	27.76	<0.01
Creatinine (*mg/dl*)	2.6a	2.7a	2.3b	14.53	<0.01
BUN:Creat.	3.7a	5.2b	7.7c	43.13	<0.01
CK[1] (*UI/l*)	745	864	698	0.40	0.67
Glucose (*mg/dl*)	156	152	162	0.74	0.48
LDH[1] (*UI/l*)	628	681	687	2.71	0.03
AST[1] (*UI/l*)	183a	182a	432b	14.16	<0.01
1995					
BUN (*mg/dl*)	11.1a	9.2a	22.9b	104.20	<0.01
Σ Protein (*g/dl*)	6.4a	7.0b	6.8b	6.82	<0.01
Albumin (*g/dl*)	3.3	3.3	3.4	1.02	0.36
γGT[1] (*UI/l*)	62.4	70.5	55.6	1.40	0.25
AST[1] (*UI/l*)	196	214	216	0.42	0.66
Ca (*mg/dl*)	10.1a	10.3a	11.5b	27.06	<0.01
P (*mg/dl*)	6.0a	5.4a	6.8b	6.17	<0.01
Na (*Meq/l*)	154a		158b	14.01	<0.01
Chl (*Meq/l*)	100		100	0.10	0.90
K (*Meq/l*)	4.8a		5.1b	4.27	0.02
Mg (*mg/dl*)	2.6a	2.9b	3.1b	16.26	<0.01
2000	Steens	John Day	Nevada		
BUN (*mg/dl*)	18.3a	23.6b	11.7c	39.21	<0.01
Σ Protein (*g/dl*)	8.4a	6.7b	6.2b	21.97	<0.01
Albumin (*g/dl*)	5.2a	4.0b	4.1b	18.23	<0.01
Creatinine (*mg/dl*)	2.2a	1.6b	2.0a	14.70	<0.01
BUN:Creat.	8.4a	14.9b	5.9c	61.73	<0.01
Glucose (*mg/dl*)	150	138	107	1.57	0.216
Σ Biliruben (*mg/dl*)	0.3a	0.1b	0.1b	28.88	<0.01
γGT[1] (*UI/l*)	52.5	74.5	50.1	2.17	0.12
AST[1] (*UI/l*)	207	263	200	1.99	0.15
Ca (*mg/dl*)	11.8a	10.0b	9.7b	9.56	<0.01
P (*mg/dl*)	7.8a	6.9a	5.1b	6.84	<0.01
Na (*Meq/l*)	162	152	147	2.20	0.12
Chl (*Meq/l*)	100a	89.8b	91.6b	3.58	0.03
K (*Meq/l*)	7.8a	4.8b	4.3b	7.63	<0.01

[1] γGT=Gamma-glutamyltransferase; LDH=Lactate dehydrogenase; ALT=Alanine aminotransferase; AP=Alkaline phosphatase; AST=Aspirate aminotransferase; SDH=Sorbitol dehydrogenase; CK=Creatine Kinase.

Only mean glucose, calcium, sodium, and potassium levels did not differ (P > 0.05) between 5 sampling events that occurred between 1989 and 2000 in the Hart Mountain population. The John Day River population, sampled 4 times between 1990 and 2000, differed (P <0.01) in mean BUN, creatinine, BUN:creatinine ratio, total bilirubin, and calcium. Steens Mountain also differed (P <0.01) in mean values for most nutritional indices (BUN, total protein, albumin, creatinine) as well as Ca and Na in 4 sampling events between 1988 and 2000. Although nutritional indices again tended to have most of the observed differences, no particular parameter tended to have higher or lower values for any given year.

Table 5. Selected parameter means through time for 3 California bighorn sheep in Oregon, 1988-2000. Means within a row with the same letter are not different (LSD, $P = 0.05$).

Population Parameter	Years Sampled 1989	1990	1994	1995	1996	*F*	*P>F*
Hart Mountain							
BUN (B, *mg/dl*)	9.1a	12.7c	9.4a	10.4a	11.8bc	6.21	<0.01
Σ Protein (*g/dl*)	6.6a	7.0b		6.6a	7.2b	6.45	<0.01
Albumin (*g/dl*)	4.0a	4.1a		3.3b	4.4c	55.64	<0.01
Creatinine (*mg/dl*)	2.3a	2.5ab	2.6b		2.0c	29.76	<0.01
B:Creat.	4.0a	5.1b	3.7a		6.0c	12.82	<0.01
Glucose (*mg/dl*)	153ab	163a	156a		137b	3.99	0.01
AST[1] (*IU/l*)	256a	324a	183ab	203ab	157c	9.88	<0.01
Ca (*mg/dl*)	9.7	10.4		10.2	12.7	1.64	0.18
P (*mg/dl*)	5.1a	7.6c		5.7ab	6.4b	9.00	<0.01
Na (*Meq/l*)	150	154		153	152	1.67	0.18
Chl (*Meq/l*)	100ab	102a		100ab	96b	11.83	<0.01
K (*Meq/l*)	4.8	5.4		5.0	5.3	0.65	0.58
John Day River	1990	1996	1999	2000		*F*	*P>F*
BUN (B, *mg/dl*)	14.4a	24.6b	24.7b	23.6b		30.39	<0.01
Σ Protein (*g/dl*)	6.8	6.9	6.8	6.7		0.20	0.90
Albumin (*g/dl*)	4.2	4.2	4.1	4.0		1.88	0.14
Creatinine (*mg/dl*)	2.2a	1.7b	1.7b	1.6b		21.99	<0.01
B:Creat.	6.7a	15.0b	14.4b	14.9b		33.08	<0.01
Glucose (*mg/dl*)	157	147	140	138		0.87	0.46
γGT[1] (*IU/l*)		60.8	55.9	74.5		1.10	0.34
AST[1] (*IU/l*)	386	190	311	263		2.40	0.08
Ca (*mg/dl*)	10.7a	10.0b	10.1b	10.0b		4.96	<0.01
P (*mg/dl*)	8.0	7.8	6.9	6.9		1.25	0.03
Na (*Meq/l*)	151a	157b	152a	152a		4.15	0.01
Chl (*Meq/l*)	98.2a	89.9b	97.4a	89.8b		3.35	0.02
K (*Meq/l*)	6.0	5.7	5.1	4.8		2.44	0.07
Steens Mountain	1988	1994	1995	2000		*F*	*P>F*
BUN (B, *mg/dl*)	12.0a	13.9a	9.2b	18.3c		24.44	<0.01
Σ Protein (*g/dl*)	7.4a		7.0b	8.4c		24.93	<0.01
Albumin (*g/dl*)	3.3a		3.3a	5.2b		208.46	<0.01
Creatinine (*mg/dl*)	2.2a	2.7b		2.2a		17.72	<0.01
Glucose (*mg/dl*)	144	152		150		0.08	0.92
γGT[1] (*IU/l*)	46.3		70.5	52.5		2.49	0.09
AST[1] (*IU/l*)	208	182	214	207		0.36	0.79
Ca (*mg/dl*)	11.1a		10.3b	11.8c		11.26	<0.01
P (*mg/dl*)	6.2ab		5.4b	7.8a		4.34	0.02
Na (*Meq/l*)	151a		152a	162b		31.08	<0.01
K (*Meq/l*)	6.6		5.4	7.8		2.97	0.06

Because only BUN was represented in all sampling events, data were only marginally sufficient for conducting stepwise linear regression to determine the usefulness of blood chemistry as a predictor of population growth. However, 2 parameters did meet minimum entry level requirements of $P = 0.11$ with BUN entering ($P = 0.11$) the first step and Total Protein entering ($P = 0.12$). The final model,

$$R_0 = 5.083 + 0.026(\text{BUN}) - 0.659(\Sigma\text{Protein}) + \varepsilon$$

explained 81% of the variation in population growth ($P = 0.08$) with 52% explained by mean BUN value.

California bighorn sheep reference values

Table 6. Normal blood serum chemistry values for California bighorn sheep populations in Oregon, 1988-2000.

Parameter	n	Normal Range	Med.	$\bar{x}$	SE	CV
BUN (*mg/dl*)	423	7 - 28	14	15.8	0.34	44.2
Σ Protein (*g/dl*)	344	5.8 - 8.3	6.9	6.9	0.05	12.1
Albumin (*g/dl*)	344	3.0 - 4.9	3.9	3.9	0.04	17.0
Globulin (*mg/dl*)	133	2.1 - 4.2	2.9	3.0	0.06	23.3
Albumin:Globulin	133	0.8 - 1.9	1.5	1.4	0.03	25.6
Creatinine (*mg/dl*)	335	1.5 - 2.8	2.2	2.1	0.02	20.6
BUN:Creatinine	334	2.7 - 17.3	6.3	8.1	0.30	59.9
CK[1] (*IU/l*)	225	235 - 2532	713	1124	99.40	133
Glucose (*mg/dl*)	335	89 - 199	152	149	2.40	29.6
Cholesterol (*mg/dl*)	110	42 - 71	58	57.6	0.90	16.1
Total Biliruben (*mg/dl*)	256	0 - 0.4	0.2	0.2	0.01	69.8
Direct Biliruben (*mg/dl*)	133	0 - 0.3	0.0	0.1	0.01	175
Indirect Biliruben (*mg/dl*)	133	0 - 0.2	0.1	0.1	0.01	71.7
γGT[1] (*IU/l*)	262	23 - 123	46.0	57.4	2.10	59.2
LDH[1] (*IU/l*)	161	534 - 1160	726	801	29.50	46.7
ALT[1] (*IU/l*)	28	26 - 60	37.5	40.0	2.30	30.1
AP[1] (*IU/l*)	133	82 - 1050	221	345	25.20	84.1
AST[1] (*IU/l*)	423	117 - 545	193	243	8.30	70.4
SDH[1] (*IU/l*)	123	7.1 - 122	24.0	40.1	5.70	157
Uric Acid (*mg/dl*)	82	0.1 - 0.6	0.2	0.2	0.02	87.6
Triglycerides (*mg/dl*)	82	71 - 422	212	212	11.10	47.4
Calcium (*mg/dl*)	344	8.9 - 12.4	10.4	10.6	0.20	35.9
Phosphorous (*mg/dl*)	344	4.0 - 9.6	6.5	6.7	0.10	32.8
Sodium (*Meq/l*)	344	146 - 164	154	153	0.60	6.7
Chloride (*Meq/l*)	344	88 - 105	99	98	0.50	9.1
Potassium (*Meq/l*)	344	4.0 - 7.2	5.0	5.4	0.10	38.0
Magnesium (*mg/dl*)	211	2.3 - 4.5	3.2	3.2	0.05	21.5
Iron (*mCg/dl*)	82	142 - 263	201	200	4.90	22.2
Σ CO_2 (*Meq/l*)	123	1.6 - 14.2	5.0	6.4	0.50	86.9

[1] CK= Creatine Kinase; γGT=Gamma-glutamyltransferase; LDH=Lactate dehydrogenase; ALT=Alanine aminotransferase; AP=Alkaline phosphatase; AST=Aspirate aminotransferase; SDH=Sorbitol dehydrogenase.

were completed for 29 parameters commonly evaluated with standard serum blood chemistry analyses (Table 6). Reference values are based on sample sizes ranging from 28 to 423 as a result of variability in specific parameters reported by different labs. However, most (79%) are based on > 100 samples with 55% of the reference values based on > 200 individual samples. Overall variability estimates (CV) for parameter values ranged from a low of 6.7% (very little variation across all samples) for sodium to a high of 175% (highly variable across samples) for direct bilirubin. Generally, diagnostic indices appeared to be more variable than either nutritional indices or mineral values.

DISCUSSION

Blood characteristics have been explored as potential indices to nutrition in wildlife for a number of years. Blood urea nitrogen (BUN) is most widely used in ruminants because it appears to be directly related to protein intake and is relatively unaffected by capture and handling stress (Harder and Kirkpatrick 1996). However, BUN may have diurnal cycles, may be affected by energy intake (Harder and Kirkpatrick 1996), and is affected by catabolic processes during prolonged periods of protein intake below that required for maintenance and seasonal fluctuation in diet (Hebert 1978, Harder and Kirkpatrick 1996). Regardless, values of blood chemistry constituents, primarily BUN, protein, cholesterol, and alkaline phosphatase have been suggested as indicative of relative nutritional differences in bighorns (Franzmann and Thorne 1970, Franzmann 1971*a*, Hebert 1978, Borjesson et al. 2000).

Five blood constituents commonly associated with nutrition (BUN, Σ protein, albumin, creatinine, and BUN:creatinine ratio: Harder and Kirkpatrick 1996, Chin 1997) differed between male and female California bighorns in Oregon. Of these, BUN and BUN:creatinine ratios were higher for males than females (Table 2). Borjesson et al. (2000) also report some differences with males having higher BUN, alkaline phosphatase, and glucose values than females. It is well documented that male and female bighorns typically segregate for most of the year (Wishart 1978, Bleich et al. 1997). Bleich et al. (1997) demonstrated that sexual segregation in desert bighorns led to dietary differences that resulted in differences in available nutrition between rams and ewes. Sexual segregation has been observed in California bighorn sheep in Oregon as well (Kornet 1978, Payer 1992). Thus, differences we observed between rams and ewes likely represent slight differences in nutrition available to the sexes. However, the large sample size available for our study resulted in high statistical power for this comparison. Although we feel these differences represent real nutritional differences, we also believe the observed differences between rams and ewes were not sufficient to result in differential impacts to the ram and ewe segments in populations we studied.

Similar to the comparison between sexes, observed differences between age class (lamb, yearling, adult) of California bighorns in Oregon tended to occur for constituents commonly used to index nutrition (BUN, protein, globulin, creatinine, BUN:creatinine, Na, Chl: Table 3). Further, lambs tended to differ from either yearlings or adults. Similar to Borjesson et al. (2000) and Kock et al. (1987*b*), we found lambs had lower total protein and lower globulin than either yearlings or adults. Kock et al. (1987*b*) also found lower BUN in lambs as well, whereas we found higher BUN levels in lambs compared to adults and yearlings. Lower total globulin levels in lambs are primarily a result of low immunoglobulin levels resulting from a developing immune system in lambs Borjesson et al. (2000). Total protein and BUN are correlated with diet (Hebert 1978, Harder and Kirkpatrick 1996). BUN also is affected by environmental factors, temporal, and diurnal cycles (Franzmann 1972, Hebert 1978, Harder and Kirkpatrick 1996). Although we found higher mean BUN values in lambs (19.3) than adults (15.7) and yearlings (16.1), we also found mean BUN values much higher than many other reports for wild bighorns (Franzmann and Thorne 1970, Davies 1976, Borjesson et al. 2000). It is possible that the higher BUN values we observed in bighorn lambs are a result of better diets on ewe/lamb ranges in Oregon compared to most other studies. Because of our large sample size, we were able to compare values in yearlings as a separate age class. Where differences occurred between age classes, the trend was for similarity in yearlings and adults. Thus we conclude that yearlings are not too different from adults physiologically as measured by blood chemistry.

Our unusually large and diverse sample

size (n=423) allowed us to compare blood constituents across distinct populations within several sampling years. In addition to finding differences in indices of diet, we also found differences in minerals. During 1994 and 1995, most nutritional indices were generally higher in the Leslie Gulch population compared to the Hart Mountain and Steens Mountain populations. During 2000, most of the same indices were higher in the John Day River population compared to either the Steens Mountain, or Nevada populations. Of those studies we reviewed, few report comparisons between distinct populations or within a population through time (Franzmann and Thorne 1970, Franzmann 1971*a*, Franzmann 1971*c*, Hebert 1978). However, many authors indicate that ungulate diet quality is reflected in blood chemistry parameters (Franzmann and Thorne 1970, Franzmann 1971*c*, Franzmann 1972, Hebert 1978, McDonald et al. 1981, Harder and Kirkpatrick 1996). It is likely that differences we observed reflect the relative differences in dietary quality available to the populations (Hebert 1978). The trend for populations associated with river corridors (Leslie Gulch and John Day River) suggests these habitats may provide better nutrition to California bighorns in Oregon.

The duration of our sampling effort also allowed us to compare changes in blood serum chemistry within 3 populations across years. Comparisons indicated significant variation through time, primarily in parameters used as indices of nutrition. Although there were exceptions (1990 on Hart Mountain, 1994 on Steens Mountain), most differences suggest nutrition was likely better for populations sampled during recent years (1995-2000) compared to earlier sampling efforts (1988-1994). As available nutrition improves, indices measurable in bighorn sheep blood serum chemistry also improve (Franzmann and Thorne 1970, Hebert 1978). Thus, differences we observed through time in this analysis likely reflect the temporal dynamics of nutrition available to the populations we sampled. Additionally, stepwise linear regression suggested the possibility of a relationship between BUN and total protein with population growth. Sample size was limited for this analysis, however, and even though the model explained 81% of the variation, it was not significant ($P > 0.10$). Further development of this data set through time may increase the predictive strength of this relationship.

Normal values and ranges for most parameters we measured are similar to other published reports (Table 7) for Rocky Mountain, California, and desert bighorn sheep (Davies 1976, Bottrell et al. 1978, Puls 1994, Borjesson et al. 2000), thinhorn sheep (Bottrell et al. 1978, Foreyt et al. 1983) and domestic sheep (Puls 1994). The greatest variation in central measures (mean or median) across studies we found was for BUN with glucose and cholesterol also varying considerably. However, our study mean of 15.8 for BUN, was well within the range reported by other authors (8.7 – 37.0). We feel the wide range of values reported for BUN, as well as glucose and cholesterol reflects the wide range of habitats and nutritional planes available to bighorn sheep.

The values we report for California bighorns provide an additional diagnostic tool for management and research. Blood chemistry results can be used when designing monitoring schedules for radio-marked sheep. Individuals with measured values outside normal ranges for specific diagnostic parameters may warrant additional monitoring efforts. Additionally, serum blood chemistry profiles may be helpful in determining cause of death, or

Table 7. Normal blood serum chemistry values from Oregon California bighorn sheep and other published reports.

	This Study		Bottrell et al. 1978 ($\bar{x}$)		Davies 1976 Rocky		Borjesson et al. 2000 Desert		Puls 1994	
Parameter	Range	Med	Rocky	Calif.	$\bar{x}$	Range	Range	Med	Bighorn	Domestic
BUN (*mg/dl*)	7.0-28.0	14.0	37.0	33.8	14.0	10-19	5.0-28.0	14.0	8.0-25.0	8.0-20.0
Σ Protein (*g/dl)*	5.8-8.3	6.9	7.1	6.2	6.5	5.6-7.7	6.0-9.3	7.4	5.0-7.0	6.0-7.9
Albumin (*g/dl)*	3.0-4.9	3.9	3.8	3.5	---	---	2.8-3.7	3.3	---	2.4-3.0
Globulin (*mg/dl*)	2.1-4.2	2.9	3.3	2.7	2.9	2.2-3.8	2.8-6.1	4.0	---	---
Albumin:Globulin	0.8-1.9	1.5	---	---	---	---	0.5-1.2	0.9	---	---
Creatinine (*mg/dl*)	1.5-2.8	2.2	---	---	2.6	2.1-3.1	1.6-2.6	2.0	---	1.0-2.9
BUN:Creatinine	2.7-17.3	6.3	---	---	---	---	2.5-14.8	7.0	---	---
CK (*IU/l*)	235-2532	713	---	---	135	49-385	175-2300	392	74-114	8-13
Glucose (*mg/dl*)	89-199	152	141	129	140	65-240	95-185	151	80-150	50-80
Cholesterol (*mg/dl*)	42-71	58	52	38	70	51-85	---	---	35-90	52-76
Σ Biliruben (*mg/dl*)	0.0-0.4	0.2	---	---	0.5	0.4-0.8	0.0-0.1	0.1	---	0.1-0.4
D. Biliruben (*mg/dl*)	0.0-0.3	0.0	---	---	---	---	0.0-0.0	0.0	---	---
I. Biliruben (*mg/dl*)	0.0-0.2	0.1	---	---	---	---	0.0-0.1	0.1	---	---
γGT[1] (*IU/l*)	23.0-123	46.0	---	---	---	---	20.0-130	36.0	---	18.0-40.0
LDH[1] (*IU/l*)	534-1160	726	---	---	344	200-555	409-788	534	268-593	60-111
ALT[1] (*mg/l*)	26-60	37.5	---	---	110	74-145	---	---	109-141	10.0-12.0
AP[1] (*IU/l*)	82-1050	221	276	356	82	33-185	73-575	166	---	70-263
AST[1] (*IU/l*)	117-545	193	---	---	212	115-525	78-312	137	130-250	68-200
SDH[1] (*IU/l*)	7.2-122	24.0	---	---	---	---	---	---	---	6.0-30.0
Calcium (*mg/dl*)	8.9-12.4	10.4	10.1	9.8	11.5	10.2-14.0	9.3-11.5	10.3	8.0-10.0	11.0-13.0
Phosphorous (*mg/dl*)	4.0-9.6	6.5	7.8	7.4	5.9	2.9-8.4	4.0-9.3	6.5	---	5.0-7.0
Sodium (*Meq/l*)	146-164	154	153	151	143	141-148	145-160	153	---	139-152
Chloride (*Meq/l*)	88-105	99	---	---	---	---	89-107	99	---	98-110
Potassium (*Meq/l*)	4.0-7.2	5.0	5.6	5.3	4.9	3.7-6.7	3.8-6.3	4.7	---	3.9-5.4
Magnesium (*mg/dl*)	2.3-4.5	3.2	---	---	---	---	---	---	0.8-3.0	2.0-3.5
Iron (*mCg/dl*)	142-263	201	---	---	---	---	---	---	---	166-222

[1] CK=Creatine Kinase; γGT=Gamma-glutamyltransferase; LDH=Lactate dehydrogenase; ALT=Alanine aminotransferase; AP=Alkaline phosphatase; AST=Aspirate aminotransferase; SDH=Sorbitol dehydrogenase.

predisposition to outside mortality factors. For example, adult ewe #00-06 captured in Nevada during winter 2000 died during transport to Oregon. Blood chemistry results revealed that values for BUN, λGT, AST, and SDH were above the normal range we observed. Subsequent necropsy revealed she died of severe cancer to the liver.

The data we report here are not without limitations. Over the duration of our sampling effort, results were obtained from 4 different laboratories without blind samples to quantify potential variation. Although most labs utilize comparable techniques and equipment, variation between labs may produce bias, thus decreasing the power (Probability of a Type II error, or β) of our comparisons. However, we feel that differences we observed between groups (age, sex, population, or temporally) were real due to the magnitude of the differences and the extremely low statistical probabilities observed for the comparisons. Our inference also is constrained by the observational nature of the data set. This is especially true for the normal values and ranges we report which do not describe critical levels. Further experimental work is required to determine these critical values, and to determine the effects of being outside the range of critical values for both individuals and populations.

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ROCKY MOUNTAIN BIGHORN SHEEP TRANSPLANTS IN HELLS CANYON

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Abstract: Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) were extirpated from Hells Canyon by the 1940s, and restoration efforts began in 1971. Translocations have resulted in 15 established herds totaling 780 bighorns. Movements and survival of transplanted sheep based on origin of transplant stock and habitats at release sites were evaluated for 4 recent releases. Three releases were successful and 1 was unsuccessful. Extensive movements to a domestic sheep allotment and/or to other sheep herds are thought to be the reason for the failed transplant. We documented movements up to 80 km (50 miles) from release sites and across major rivers and reservoirs. Sheep from alpine herds seemed to move more than sheep from a canyon population. Migratory alpine sheep may be more suitable as supplements to existing herds. Due to the historically high potential for transplant failure throughout the west, we recommend radiocollaring and regularly monitoring sheep following release in order to determine causes for success or failure.

Translocation of bighorns to historic habitat has been widely used by wildlife managers to increase wild sheep numbers and distribution. Transplants are very popular with the public and have been successful in restoring bighorns to former habitat. Rocky Mountain bighorn sheep populations increased from an estimated 9,700 in 1960 (Buechner 1960) to nearly 34,500 in 1998 (Toweill and Geist 1999). Much of this increase was due to transplants. There have also been many transplant failures (Coggins and Matthews 1996, Enk et al. 1998, Singer et. al. 1999). This study was initiated to intensively follow 4 transplants to determine mortality rates, sheep movements, productivity, and other factors affecting the success of translocations.

HISTORY

Rocky Mountain bighorn sheep were native to Hells Canyon and were thought to be very abundant (Bailey 1936). Archaeological investigations indicate bighorn bones were the most abundant ungulate bones recovered at Native American campsites in Hells Canyon (Randolph and Dahlstrom 1977). Wild sheep were totally extirpated from Hells Canyon in Oregon, Idaho, and Washington by the mid-1940s. Diseases contracted from domestic sheep were believed to have been the major cause of the extinction of Hells Canyon bighorns (Coggins 1980).

Bighorn sheep restoration in Hells Canyon began in 1971 with the release of 40 animals from Jasper National Park, Canada (Coggins and Matthews 1996). Between 1971 and 1999, 415 sheep have been released in Hells Canyon and the surrounding area from 10 source populations, resulting in 15 established herds (Hells Canyon Bighorn Sheep Recovery Committee, unpublished reports 1996, 1997, 1998, 1999). The March 2000 population estimate was 780 animals (Hells Canyon Bighorn Sheep Recovery Committee, unpublished data). This study evaluates 4 recent transplants and reasons for success or failure. Information from other earlier transplants in the Hells Canyon area is also discussed. The project is part of the Hells Canyon Bighorn Initiative to restore extirpated wild sheep to Hells Canyon.

STUDY AREA

Hells Canyon of the Snake River is located in Oregon, Idaho, and Washington. Elevations range from about 240 m (800 ft) near Lewiston, Idaho to above 2740 m (9,000 ft) in the Seven Devils Mountains, Idaho and Wallowa Mountains, Oregon. Much of the area is public land administered by the Wallowa-Whitman National Forest. Grazing by cattle occurs in portions of Hells Canyon but most domestic sheep allotments have been eliminated on public land. Historically, pneumonia outbreaks, believed to be caused by contact with domestic sheep or goats, resulted in serious adult losses and subsequent depressed lamb survival in some transplanted herds (Coggins and Matthews 1996).

Terrain is steep and sharply dissected. Perennial bunchgrass plant communities interspersed with cliff rock, Douglas fir (*Pseudotsuga menziesii*) and Ponderosa pine (*Pinus ponderosa*) stringers typify Hells Canyon. Climate is characterized by light precipitation. Summers are hot and winters mild (Johnson and Simon 1987).

METHODS

Between 1997 and 1999, 53 Rocky Mountain bighorns from 3 source herds (Cadomin Mine, Hinton, Alberta; Spences Bridge, British Columbia; and Lostine, Oregon) were translocated to 3 vacant sites: Muir Creek, Oregon; Big Canyon, Idaho; and McGraw Creek, Oregon, and 1 occupied site: Asotin Creek, Washington. A summary of sheep released follows:

1. Asotin Creek: 10 animals (8 ewes, 2 rams) from Spences Bridge supplemented an existing herd of 10 sheep in December 1997.
2. Big Canyon: 15 animals (11 ewes, 4 rams) from Spences Bridge released at a vacant site in December 1997; supplemented with 6 additional sheep (3 ewes 3 rams) from Hinton in February 1999.
3. Muir Creek: 13 animals (9 ewes, 4 rams) from Spences Bridge released at a vacant site in December 1997; supplemented with 14 sheep (11 ewes 3 rams) from Hinton in February 1999.
4. McGraw Creek: 15 animals (9 ewes, 6 rams) from Lostine released at a vacant site in January 1999.

All sheep, except 4 lambs, were equipped with mortality-sensing radio-collars and monitored by aircraft or from the ground at least every 2 weeks. All animals were ear-tagged with individually numbered Alflex tags to assist in ground identification. Animals with transmitters on mortality signal were located as quickly as possible to determine the cause of death. Ewes were located approximately weekly during lambing to determine productivity.

RESULTS

Adult survival and dispersal

Spences Bridge Source Population

Thirty of 38 Spences Bridge sheep (79%) released in December 1997 were still alive in April 2000 (2 years 4 months post release).

Survival was highest for sheep released at Big Canyon (88%) (Fig. 1). One ram lamb released at Big Canyon dispersed to another bighorn herd (the Lower Hells Canyon herd). Survival of sheep released at Asotin Creek was lowest (60%) and no sheep dispersed to other herds. Survival at Muir Creek was intermediate (77%). Two ewes from Muir Creek dispersed to another herd (Imnaha). One of these ewes died and status of the other is unknown due to radio failure.

Causes of mortality were mostly unknown (N=5) because scavengers or predators consumed the carcasses prior to their being examined. Two rams died within 2 weeks of release. Documented causes of mortality included 1 cougar kill, 1 Nez Perce tribal hunter kill, and 1 case of bacterial meningitis.

During the first year post-release, 24% (N=9) of bighorns moved from the release site in 4 independent movement events. Seven (18%) of the 38 released sheep crossed the Snake River in 2 movements. Three bighorns (8% of those released: 2 ewes and 1 ram lamb) permanently moved to other herds, and 1 subsequently died.

Hinton Source Population

Twenty bighorns from the Cadomin Mine, Hinton, Alberta were released at Muir Creek (N=14) and Big Canyon (N=6) in February 1999. Sixteen (80%) were alive in April 2000 (1 year 4 months post release). All 6 sheep released at Big Canyon survived, while 4 (29%) Muir Creek sheep died. One ewe died from unknown causes shortly after release (completely scavenged), and 3 sheep dispersed to other areas and died: 1 cougar kill, 1 road kill, and 1 pneumonia.

By October 1999, 58% (N=11) of the Hinton sheep had traveled away from release areas in 12 independent movement events (1 or more sheep moving away from the release site). Five bighorns (25% of those released) permanently moved to other herds and 4 subsequently died. Median distance moved was 21 km (13 miles) for both dispersal and exploratory movements. The maximum distance moved was 80 km (50 miles), by an adult ewe. Sheep crossed the Snake River in half of the movements (27% of sheep released). Nearly all rams exhibited some major movements away from release sites, but only 2 of 6 relocated permanently. Two yearling rams dispersed to the Imnaha herd where 1 was later killed by a cougar. About half of the ewes made major movements, but only 2 dispersed to other ranges. One yearling ewe dispersed to the Big Canyon herd and survived. An adult ewe dispersed to the McGraw herd where she died of pneumonia.

Lostine Source Population

Fifteen bighorns from the Lostine herd were transplanted to McGraw Creek in January 1999. Nine (60%) were alive in April 2000 (1 year 5 months post release). The sheep were released on the Oregon side of Hells Canyon Reservoir where no domestic sheep are present. Unfortunately, an active summer domestic sheep allotment exists on the Idaho side. Five rams and 4 ewes from the transplant crossed the reservoir and were located at least once on the active domestic sheep allotment. While bighorns were never seen making contact with domestic sheep, they were located within 1 km of a range band on several occasions. Two bighorn rams that had visual symptoms of respiratory disease (coughing, sneezing, and nasal discharge) were shot in August 1999. Antibody titers to Parainfluenza-3 virus were elevated (1:64) from those at capture in January (1:8), but necropsy revealed no gross or histological evidence of pneumonia. High summer lamb mortality and observations of coughing indicate this herd suffered respiratory disease problems likely related to domestic sheep contact, either directly or through contact with other infected bighorns. Two dead bighorns (1ewe, 1 ram) were recovered in poor condition but no evidence of pneumonia was found. Another ewe appeared to be killed by a cougar.One ewe and a ram dispersed to the adjacent Upper Hells Canyon herd.

Lamb survival

Average lamb survival to 8 months of age was highest for the Spences Bridge source population (67%) and lowest for the Lostine sheep released at McGraw Creek (0%) (Table 1). Lamb survival of Spences Bridge ewes (the only release where a comparison could be made) was lower the year immediately after the transplant than the following year. Lamb survival was also lower for sheep released at Muir Creek than Big Canyon, possibly because more yearlings were released. They were less experienced and may have had smaller lambs. More Hinton ewes were released at Muir Creek and they moved more which may also have increased lamb losses. No McGraw Creek lambs survived in 1999, although all 9 ewes released had lambs. Based on movements and disease-related mortality in adults, we believe disease accounted for most of the lamb mortality in that herd.

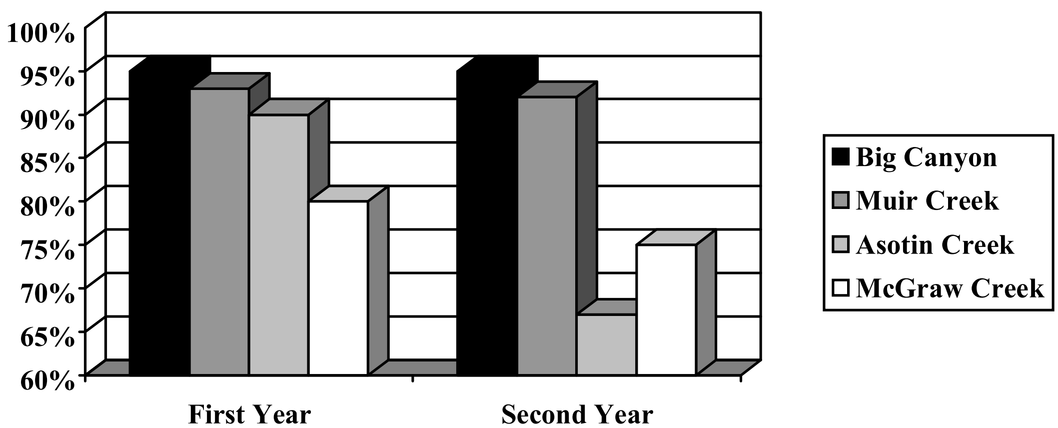

Fig. 1. Annual survival of transplanted bighorn sheep from 1998 to 2000.

Table 1. Hells Canyon lamb survival to 8 months of age by release site and source population.

Year	1998	1999		
Source population	Spences Bridge	Spences Bridge	Hinton	Lostine
Release site				
Big Canyon	67%	91%	67%	
Muir Creek	29%	71%	38%	
Asotin Creek	71%	63%		
McGraw Creek				0

DISCUSSION

During previous transplants, dispersal has been a major cause of transplant failures in Hells Canyon. Dispersal of individuals has varied considerably depending upon source of transplant stock. Sheep from Salmon River, Idaho and Wildhorse Island, Montana source populations have moved the least. Source stock from other herds have moved more frequently with some Hinton and Lostine bighorns moving great distances (Coggins and Matthews 1996).

Although the Spences Bridge sheep were released into unoccupied habitat and the Hinton transplant was a supplement, the sheep transplanted from Hinton moved more often, and were slightly more likely to disperse to adjacent herds than the sheep from Spences Bridge. Another 37 Hinton bighorns were released at Minam River, Oregon and Big Sheep Creek, Oregon in February 2000. These were vacant sites, and preliminary information indicates dispersal to locations greater than 71 km (44 miles) by air. While it is still unknown if dispersers will return to release sites, some bighorns moved to agricultural areas and towns, increasing their risk of pathogen transmission from farm flocks of domestic sheep or of being hit on highways. Because of their propensity to disperse, Hinton stock may be used more successfully to supplement small, established herds.

Prior to this transplant, no radio-collared resident sheep (mostly ewes) in 3 herds (Lower Hells Canyon, Oregon, Redbird, Idaho, or Black Butte, Washington were documented crossing the Snake River. Sheep did cross the Snake River during previous transplants and sheep released in the three study herds on the Snake River initially repeatedly crossed the Snake River or Hells Canyon reservoir. Rams continue to move readily across the Snake River and may summer with one herd and winter with another. Both ewes and rams cross Hells Canyon Reservoir.

These movements may add to the genetic exchange between bighorn herds but also increase the potential for disease transmission. This is especially true for the McGraw Creek transplant, where 53% of the bighorns have crossed Hells Canyon Reservoir at least once. In some cases, ewes lambed on one side of the reservoir and swam with new lambs back to the other side. This is of major concern because they moved to an active domestic sheep allotment on the Payette National Forest.

Although predation can be a significant source of mortality in transplants, predation on the 4 study herds was not a significant factor affecting transplant success. Annual survival rates were 90% or greater for Big Canyon, Muir Creek and Asotin Creek the first year post-release. Disease and management removals in the McGraw Creek herd resulted in a 67% annual survival.

MANAGEMENT IMPLICATIONS

Many early transplants in Hells Canyon had little follow-up monitoring, and if populations failed to become established, the reasons for failure were unknown. This study documented that the primary reason for failure in one transplant was extensive post-release movements increasing the risk of contact with domestic sheep and disease transmission. This resulted in elevated adult mortality and complete loss of lambs.

Major rivers and reservoirs frequently are considered barriers to bighorn movements. This appears to be true for ewes in some resident herds. However, following release, some transplanted bighorns repeatedly crossed the Snake River or Hells Canyon Reservoir. This was especially important for the McGraw herd because of movement to a domestic sheep allotment on the east side of the reservoir.

We observed possible differences in source populations that could affect transplant success. Extensive movements by transplanted individuals can result in failure because few sheep remain near the release sites. Matching habitat characteristics of the source herd with the release area may improve the chance of successful population establishment. Also, supplementing small, established herds rather than releasing sheep into vacant habitat may be more successful with source stock known to be dispersers.

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AN UNUSUAL CONTAGIOUS ECTHYMA OUTBREAK IN ROCKY MOUNTAIN BIGHORN SHEEP

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Abstract: An unusual contagious ecthyma outbreak was observed in a herd of approximately 160 Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in Custer State Park, South Dakota. Symptomatic lesions were observed from February 1997 through January 1998, with all age and sex classes affected. Lambs were severely affected. The most heavily infected lambs exhibited lesions over the majority of their bodies, and associated swollen hooves impeded movement. Previous outbreaks in Custer State Park began in fall or winter and lasted 2-4 months, with severe infections never documented. Lamb survival is usually low in this herd and lamb:ewe ratios in 1997 dropped from roughly 88 lambs:100 ewes in June to 16 lambs:100 ewes by November. Descriptive data on infected lambs suggest that the virus contributed to this mortality. The prevalence, duration, and severity of this outbreak raises questions regarding the length of immunity gained from previous contagious ecthyma infections as well as the influence of physical variables on disease progression.

Contagious ecthyma (CE), otherwise known as orf, soremouth, or pustular dermatitis, is a highly infectious viral disease of the parapox group. The virus is characterized by elevated lesions that predominately affect the epithelial tissue of the lips, udders, hooves, and genitalia (Blood 1971, Lance 1980). Lesions develop rapidly and, in uncomplicated cases, healing is normally complete in 6 weeks (Lance 1980, Jessup et al. 1991). Outbreaks in a population are cyclic, may be indicative of long-term low stress levels, and are symptomatic of poor herd condition (Lance 1980).

In North America, CE was first recognized in a flock of domestic sheep (*Ovis aries*) in 1929 (Howarth 1929). Rocky Mountain bighorn sheep in Banff National Park, Canada, were the first North American wild ungulate to be documented with an infection (Connell 1954). Outbreaks in other wildlife species include California bighorn sheep (*O. c. californiana*; Blaisdell 1976), Dall sheep (*O. dalli;* Smith et al. 1982), mountain goats (*Oreamnos americanus;* Samuel et al. 1975), Himalayan tahr (*Hemitaragus jemlaicus*), chamois (*Rupicapra rupricapra*), steinbock (*Raphicerus campestris;* Kater and Hansen 1962), musk ox (*Ovibos moschatus;* Kummeneje and Krogsrud 1978), and reindeer (*Rangifer tarandus;* Kummeneje and Krogsrud 1979). In addition, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), wapiti (*Cervus elaphus;* Lance et al. 1983), and moose (*Alces alces;* Zarnke et al. 1983) have been infected experimentally.

In Custer State Park (CSP), South Dakota, CE was first documented in Rocky Mountain bighorn sheep in 1982. This outbreak was followed by three others in 1988, 1993, and 1997. The last outbreak was unusual for this herd in its prevalence, duration, and severity, and a descriptive study was begun to document its course. Funding for this study was provided by Federal Aid administered by South Dakota Game, Fish, and Parks and Custer State Park.

STUDY AREA AND METHODS

Custer State Park is located in the Black Hills in the southwestern corner of South Dakota. The park encompasses a 29,500 ha area that ranges from savanna grassland at 1.13 km elevation to rocky crags at 2.07 km elevation (Shave 1983). Ponderosa pine (*Pinus ponderosa*) is the dominant overstory species throughout the bighorn sheep range, with riparian areas containing primarily bur oak (*Quercus macrocarpa*) and paper birch (*Betula papyrifera*). Twenty-two Rocky Mountain bighorn sheep were introduced into the park in 1964 from the Whiskey Mountain herd in Wyoming. This herd has grown to approximately 160 animals, divided into 3 subherds.

Descriptive data on the CE outbreak were collected from June 1997 to January 1998 in conjunction with a bighorn sheep demographic study. During herd composition counts, each sheep was examined with binoculars for characteristic lesions. Age and sex of the sheep, location of lesions, other physical ailments, and notes on behavior were recorded. When possible, characteristics such as broken horns were used to identify individuals. The percent of lactating ewes in June and July was used to estimate the number of lambs produced, and total herd composition counts in November and December were used to calculate lamb survival. Three lambs that were severely affected were necropsied.

RESULTS

Ewes and Yearlings

Park employees noted symptomatic lesions on a small number of ewes and yearlings from February to March in all 3 subherds. After March, visible lesions were not observed on ewes or yearlings until late summer. On 22 August a ewe was seen with small lesions on her lips and a second infected ewe was seen on 14 October. From that date, infected ewes were seen with increasing frequency through December. Infections were limited to the muzzle, with infections ranging from small lesions on the lips to scabs covering the entire muzzle. Few infected yearlings were noted from September through November. Most yearling infections appeared mild, although one female did have lesions surrounding both eyes.

Lambs

In late June, composition counts and observations were begun in the subherds as part of a pilot study on lamb mortality. On 7 July characteristic lesions were seen on a lamb, whose hoof was scabby and bleeding. Infected lambs were seen through the summer and fall, with symptoms ranging from scabby lips to lesions covering most of the body. Infected lambs were not seen after November. Three lambs with severe infections were recovered and necropsied. Three additional dead lambs with small lesions on their lips were found but they were too decomposed to necropsy.

Necropsy #1 (17 July) A female lamb approximately 1 month old was found lying on a trail, unable to stand. Two hooves were swollen, 2 were split open and infected with maggots, and scabs were located around the coronet, on the lips and muzzle, and a few on the sides of its body. The lamb died within an hour of being located and was taken to Fall River Veterinary Clinic to be necropsied. No additional abnormalities were found and samples of the lesions and all major organs were sent to South Dakota State University (SDSU) and the National Veterinary Services Laboratory. Both labs identified a virus with morphological characteristics compatible with contagious ecthyma through electron microscopy. The lamb's rumen was 3/4 full of grass and contained a small amount of milk. Information on the dam's infection status or lactating condition was not available.

Necropsy #2 (1 August) This female lamb was between 1-2 months old and had been dead for 24-48 hours when it was located. All 4 hooves were infected around the coronet, and 1 was split open and infected with maggots. Lesions were also present around its lips and muzzle. Decomposition hampered the necropsy and only tissue samples from the lips were sent to SDSU for virus identification. The lab determined that a virus was present but the tissue was too autolyzed to make a positive identification. A fecal sample was processed for lungworm larvae and none were found. The lamb's rumen was full of grass. The dam exhibited no visible symptoms of CE and had a shrunken udder.

Necropsy #3 (4 September) This lamb was euthanized due to the severity of its infection. Approximately 2 months old, the female lamb could barely walk when it was discovered. All 4 hooves were infected, with 1 split open and infected with maggots. Scabs were located from the coronet past the ankle on all 4 legs, with occasional scabs up to the knee. The muzzle was completely covered with scabs and the eyes were surrounded with scabs. Both ears were almost detached at the base due to the depth of lesions and necrosis present. Lesions literally covered the body, with notable ones along the spine, sternum, and at the base of the tail. On the rest of the body, you could part the hair and see scab material. Samples of all the major organs, the head, all four legs, and major lesions were sent to SDSU. The spleen had marked lymphoid depletion, and electron microscopy suggested contagious ecthyma. A fecal sample was processed for lungworm larvae levels and it contained 11 LPG of *Muellerius capillarius.* The dam exhibited no external CE symptoms and the lamb's rumen was full of milk.

Rams

Rams of all classes (after Geist 1971) were observed with characteristic lesions from October through January 1998. Similar to ewes, infections on the muzzle ranged in intensity and one ram was observed with an infected hoof.

Infection rates

Without individual markers, it was not possible to track how many sheep in each sex/age class were infected over time or how long individual sheep were infected. Descriptions of individual infections were used to create a minimum count (Table 1). If a sheep with a similar infection was documented at any time later in the outbreak, it was not counted. This is a conservative count and the numbers were likely much higher.

Lamb Survival

An estimated 88% of ewes produced a lamb (88 lambs:100 ewes) based on 57 subherd observations in June and July. Subherd counts in October and November, when large groups were visible, were used to estimate the number of ewes and lambs in the herd. Based on an estimate of 93 ewes and 15 lambs, the lamb:ewe ratio in November was 16 lambs:100 ewes. The fall yearling:ewe ratio was 25 yearlings:100 ewes. The fall lamb ratio was lower than has been previously documented in the park (Table 2).

Table 1. Minimum counts of Rocky Mountain bighorn sheep infected with contabious echthyma during 1997 outbreak in Custer State Park, South Dakota.

	June - September	October-January[a]	Total
Lambs[b]	13	7	20
Yearlings[c]	1	1	2
Ewes	3	30	33
Rams	0	5	5

[a]If a sheep with a similar infection was counted in summer, it was not included in fall count.
[b]Count for 1997 lambs, does not include 1996 lambs infected in February or March.
[c]Count for 1997 yearlings, does not include 1996 yearlings infected in February or March.

Table 2. Lamb:ewe and yearling:ewe ratio counts for Rocky Mountain bighorn sheep in Custer State Park, South Dakota.

Year	Lambs:ewes	Yearlings:ewes
1983	45:100[a]	19:100[b]
1984	36:100[a]	21:100[b]
1985	42:100[b]	23:100[b]
1987	39:100[b]	20:100[b]
1988	77:100	24:100[b]
1989	42:100	
1997	16:100[b]	25:100[b]

[a]Ratio counts from November
[b]Ratio counts from August
[c]Ratio counts from January

DISCUSSION

The primary difference between the 1997 outbreak and the three previous infections in CSP was the effect on the new lamb crop. The 1982, 1988, and 1993 outbreaks occurred only during fall or winter, with no severe infections reported. Severe infections in lambs are not exceptional (Blood 1971, Samuel et al. 1975, Dieterich et al. 1981, Zarnke et al. 1983), but it was unique to the outbreaks in CSP. Additional underlying stress factors, as well as general poor herd condition, have been offered as explanations for other severe infections (Samuel et al. 1975, Lance 1980, Jessup et al. 1991, L'Heureux et al. 1996) and seems a likely explanation for the CSP outbreak. The CSP bighorn sheep herd has remained static at 120-160 animals since 1975, and periodic counts and employee observations indicate lamb survival has been low throughout this time (CSP, unpub. data). Lungworm infections, poor nutrition, and limited genetic variability are some of the factors that CSP has identified as potential limiting factors to lamb survival, all of which might explain the 1997 lamb crop's vulnerability to CE.

Lungworm Infections

Lungworms can adversely affect lambs directly through infection or indirectly by reducing nutritional condition of the ewes. Infections by lungworms can dispose bighorn sheep to viral and bacterial pneumonia (Buechner 1960, Forrester 1971, Stelfox 1971, Hibler et al. 1972, Demartini and Davies 1977) and the resulting lungworm-pneumonia complex has been implicated in several catastrophic lamb die-offs (Hibler et al. 1972, 1974; Woodward et al. 1974; Spraker 1979; Spraker and Hibler 1982). While pneumonia has never affected this herd, transplacental migration of *Muellerius capillarius* has been documented (Brundige 1985) and lungworm infections might be depressing lambs' immune responses. Furthermore, high parasitic loads of the ewe during gestation may increase metabolic demand for maintenance and may result in poor condition ewes (Festa-Bianchet 1991). In turn, these ewes may produce smaller, less viable young that will have greater difficulty coping with severe weather, disease, and parasites (Geist 1971). The lungworm *Muellerius capillarius* has been considered ubiquitous in this herd since 1984 (Pybus and Shave 1984) and LPG >4000 have been reported (Brundige 1985).

Poor Nutrition

Inadequate nutrition during gestation and lactation may result in weaker lambs. Udder size and lactation capacity (Thomson and Thomson 1949, 1953), as well as the onset of copious lactation and the rate of milk secretion (McCance 1960), are negatively affected by poor nutrition during gestation. When less milk is available, lambs may graze earlier and more intensely. Horejsi (1976) found that lambs in a low survival year tried to increase forage intake when the milk supply became inadequate, but by then forage quality had declined. Low milk intake and early reliance on poor forage resulted in retarded growth, a determinant of lamb mortality during his study. Severe lesions on lambs in CSP did not appear to impact their ability to feed, but several lambs were observed vigorously eating grass within 1-2 months of birth. Additionally, descriptive data from a pilot study in 1997 suggests that the bighorn sheep in CSP grow slower and reach a smaller size than those in areas with higher lamb survival (Merwin 2000).

Limited Genetic Variability

In 1990, Fitzsimmons (1992) found that the bighorn herd in CSP had an effective population size of 21, with an estimated herd size of 145 animals. The CSP herd also had significantly lower heterzygosity than its founder herd. Franklin (1980) recommend an effective population size of $\geq$ 50 animals in order to maintain genetic variability over the short term and a herd of > 500 to reduce genetic loss over the long term. Factors related to reproduction and viability of offspring are described to be the first factors depressed through an increase in homozygosity (Farnsworth 1978).

The duration of the outbreak was also unique for this CSP infection, and potentially for any CE outbreak. Lesions were seen for nine months between February 1997 and January 1998, although presumably some animals in the herd were likely infected between April-June. Again, why this outbreak was unique is linked to the infection of the new lamb crop. Lambs carried the infection through most of the summer, while yearlings and adults exhibited symptoms in the previous winter and proceeding fall. In addition, the prevalence of the infection appeared unusual compared to other CSP outbreaks. The actual percentage of the population that was infected, or the duration of individual infections, was unknown. However, given the duration of the outbreak and the consistency with which infected sheep were seen, either a smaller number of individuals were infected for much longer than the typical 4-6 weeks (Lance 1980, Jessup et al. 1991) or a majority of the herd was infected. It seems more likely that the latter is true, given the minimum number of sheep infected (see Table 1). If a majority of the herd was infected in 1997, and given that the last CE infection was in 1993, immunity to CE may be short term (Lance, personal communication) rather than long term (Blood 1971, Samuel et al. 1975, Zarnke et al. 1983, L'Heuruex et al. 1996). The prevalence of the infection supports that lambs are not protected with colostrum from infected dams (Kerry and Powell 1971).

This latest CE outbreak has emphasized the need to investigate the factors affecting lamb survival in CSP. Several potential factors, including those mentioned previously, are being examined in two separate studies. Through these investigations, we hope to gain insight in how to better manage the bighorn sheep herd for increased lamb survival and overall herd condition.

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Biennial Symposium Northern Wild Sheep and Goat Council 12:83.

NEW HOST AND GEOGRAPHIC RECORDS FOR *PROTOSTRONGYLUS STILESI* AND *PARELAPHOSTRONGYLUS ODOCOILEI* IN DALL'S SHEEP FROM THE MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES, CANADA

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Abstract: We examined Dall's sheep (*Ovis dalli dalli*) feces, collected from July to October, 1997, at four sites (ca. 63-65^{o}N; 128-130^{o}W) in the northern Mackenzie Mountains, Northwest Territories (NWT), Canada, for parasites using Baermann and modified Wisconsin techniques. First-stage larvae (L1) representing a minimum of 2 genera and species of protostrongylids were recovered: (1) spike-tailed L1 were indistinguishable from *Protostrongylus* sp. (prevalence 74%, 0.2-700 larvae per gram (LPG)); and (2) dorsal-spined L1 were morphometrically most similar to *Parelaphostrongylus odocoilei* (prevalence 77%, 0.2-967 LPG). Subsequently, adults of *Protostrongylus stilesi* were recovered from the lungs of 4 hunter-killed sheep in 1997 and 1998, and adults of *P. odocoilei* were recovered from the skeletal musculature of 6 naturally infected Dall's sheep ewes in October 1998 and April 1999. Lesions caused by *P. stilesi* were found most commonly in the dorso-caudal regions of the diaphragmatic lobes. Histologically the adult parasites, eggs, and larvae were associated with a severe, locally extensive granulomatous reaction. In contrast, eggs and larvae of *P. odocoilei* were associated with a mild to moderate multifocal, granulomatous reaction throughout all lung lobes. In the skeletal muscles, adults of *P. odocoilei* were associated with grossly visible hemorrhages and localized myositis. The findings of *P. stilesi* and *P. odocoilei* in Dall's sheep from the Mackenzie Mountains, NWT, represent new host and geographic records, and the first confirmed identifications of protostrongyles in thin-horned sheep. The presence of both these parasites in single hosts is unique and the possible synergistic effects of these combined infections for individual hosts and for host populations warrant further consideration.

Biennial Symposium Northern Wild Sheep and Goat Council 12:84.

PRELIMINARY EVALUATION OF TRACE ELEMENT LEVELS AND PATHOGEN EXPOSURE IN HELLS CANYON BIGHORN SHEEP

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Abstract: What are "normal" levels for trace elements in wild sheep? What is the relationship between trace element levels, exposure to respiratory pathogens, and demography in bighorn sheep? Antibody titers to respiratory diseases, blood and liver selenium and trace mineral levels of bighorn sheep captured or recovered in 6 Hells Canyon herds 1997-2000 are compared to herd demographic parameters including lamb:ewe ratios and rate of increase. Pathogen exposure and trace element levels observed in sheep in Hells Canyon are also compared to those observed in bighorn sheep in other areas.

Biennial Symposium Northern Wild Sheep and Goat Council 12:85.

WHAT MICROSATELLITES CAN TELL US ABOUT DISEASE RESISTANCE IN FREE-LIVING SHEEP POPULATIONS: THE GENETICS OF RESISTANCE TO NEMATODES IN NATURALLY PARASITISED SOAY SHEEP FROM ST. KILDA, SCOTLAND

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Abstract: Microsatellites can be applied to assess neutral genetic variation within or among individuals and populations, they provide markers useful for deriving pedigree relationships, and they can act as markers for regions of the genome containing QTL or candidate genes of importance. Here I will discuss how microsatellites have been applied in these three ways to study the genetic basis of resistance to gastrointestinal nematode parasites in an unmanaged population of feral Soay sheep on the island of Hirta in the St. Kilda archipelago, Scotland. Soay sheep are naturally parasitised by gastrointestinal nematodes of the genus *Teladorsagia*, the most important nematode in European domestic sheep. These worms cause damage to the gut and nutrient deficiency, and contribute to over-winter mortality during years of harsh weather and high population density. In Soay sheep parasitism can be regularly monitored by counting eggs in faeces (FEC) non-invasively. Three questions were addressed in this project using microsatellite DNA information: i) is there heritable variation for resistance, ii) is resistance compromised by inbreeding, and iii) what genes are associated with resistance? Since 1985, the paternity of 68% of 2,020 sampled lambs has been determined using a panel of 12-17 microsatellite DNA markers. This information was combined with 1,690 known mother-offspring relationships to produce a pedigree of the population. We estimated quantitative genetic parameters for FEC using REML. There was significant heritable variation for FEC (h^2 = 0.09 in males, 0.19 in females). Maternal effects were higher in females (0.20 vs. 0.07) suggesting that exposure to parasites and infection may be partly mediated by the maternal environment (i.e. shared home range use). Average individual heterozygosity (*H*) at the microsatellite loci used in the paternity analysis also provides a measure inversely correlated with inbreeding. *H* was negatively associated with FEC indicating that relatively inbred sheep are more susceptible to parasitism by nematodes. These individuals were also less likely to survive harsh winters due to their increased parasite burdens, suggesting that parasites mediate natural selection against inbreeding. Finally, we typed Soay sheep at a diallelic microsatellite locus located in the interferon gamma gene which is associated with resistance to nematode infection in domestic sheep. One allele conferred reduced FEC and increased levels of immunoglobin A in young Soay sheep. In the Soay sheep project, microsatellites have proven to be powerful and flexible tool for unravelling the genetics of a complex and important phenotypic trait. In principle, these approaches can be applied to any other ungulate population where DNA samples can be obtained and individuals can be monitored if we utilise the domestic sheep and cattle genome maps as a source of informative markers.

Biennial Symposium Northern Wild Sheep and Goat Council 12:86-87.

WORKING SESSION
Designing a protocol: What should you do if you are faced with a bighorn sheep die-off?

MODERATOR: **Glenn Erickson**

Panel Members: **Glenn Erickson, Montana**
Vic Coggins, Oregon
Kurt Alt, Montana

At the 12th Northern Wild Sheep and Goat Council symposium held in Whitehorse June 2000, a special workshop devoted to developing a protocol to deal with with a bighorn sheep die-off was conducted. Each panel member reviewed their experience with bighorn die-offs and any actions that were taken during the respective die-offs. A general panel/audience discussion followed.

Needed action items in development of a "Die-off Protocol" were identified.

1. Develop a list of contact people (veterinarians and experienced biologists) for field managers to contact when they are involved with a die-off.

2. Need to review past die-offs and identify those factors involved. Also identify similarities among die-offs, such as:
   - domestic sheep contact
   - identified stress factors
   - habitat factors (especially relating to herd size and range carrying capacity)
   - herd health and lung worm prevalence

3. Develop a standardized response procedure including "dos and don'ts"
   - Give long lasting antibiotics (LA-200 or similar). Do not administer by darting because it hasn't been effective.
   - Medicated feed might work if bighorns are habituated to site; probably will not work for herds not habituated to protein blocks, salt or pelleted feed.
   - Do not capture and pen sick sheep for treatment; results were devastating.
   - Plan on any treatment activity being very expensive.
   - At this time, there is no vaccine available for *Pasturella* infections.
   - Develop a protocol to identify needed blood/tissue samples to be taken during a die-off.
   - If you are contacted for comments on a die-off in another area, be extremely careful about criticizing their response/treatment activities since much is not known about how to treat animals or react to the situation.

4. Need to develop recommendations on preventative activities that should be done to prevent die-offs.
   - Prevention of domestic sheep contact.
   - Identify options or techniques for treating lungworm.
   - Identify what should or should not be considered an interaction/contact between domestic and wild sheep.
   - Identify those species known to cause die-offs in wild sheep (domestic sheep, exotic sheep, goats). Identify those species not known to cause die-offs (llamas, horses, cattle).
   - Develop guidelines for field managers to use in responding to agencies or individuals wanting to use domestic sheep or goats for weed control or silvicultural practices near wild sheep habitat.

5. Need to develop statement on how to deal with stray wild sheep.
   - Oregon: removes strays (rule not policy); catch them if possible but if they might escape they can be killed. Have extended authority to the public to remove the animal, but this authority is seldom used.
   - Idaho: removes strays
   - New Mexico: removes strays
   - Wyoming: removes strays; identified a problem that woolgrowers tend to not notify the department if strays are observed with domestic sheep.

6. Need to develop an experimental design to test potential treatment activities and measure the effectiveness of each treatment.

7. Need to make suggestions on how to coordinate with woolgrowers and develop mutually beneficial preventative actions.
   - How do we open the lines of communication?
   - Use the FNAWS brochure as a handout; saturate specific areas

Biennial Symposium Northern Wild Sheep and Goat Council 12:88-100.

COHORT VARIATION IN HORN GROWTH OF DALL SHEEP RAMS IN THE SOUTHWEST YUKON, 1969-1999

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Abstract: Horn growth of 2481 Dall sheep (*Ovis dalli*) rams was measured as part of harvest assessment in the southwest Yukon for cohorts born between 1969 and 1992. Estimated volumes for annual horn growth increments were based on measurements of annual horn segment lengths and their annual base circumferences. Poor horn growth was observed in 1972, 1982, and 1992 in rams of all age classes, except lambs. In general, lambs showed little variability between years, because growth during the first summer is negligible compared to subsequent years and horn tips of older rams are worn. Above-average horn growth was observed in 1977, 1978, 1989, 1994, 1995, and 1996 for rams from all cohorts. At 8 years there were significant between-cohort differences in total horn volume depending on year of birth. Good or poor years have dramatic cumulative effects on horn growth, depending on the age and growth stage of the cohorts when good or poor growth years occur. Over 31-years (1969-1999) there was a significant '10-year' periodicity in horn growth, which was consistent across all age classes and all cohorts during this period. Annual horn growth increments appear to provide an integrated climate signal that is related to precipitation and temperature cycles which likely influence plant productivity. This predictable pattern provides a context for the Yukon's sheep management program.

Key words: Dall sheep rams, *Ovis dalli*, Yukon, horn growth, cohort variation, periodicity

Climate variability has a strong influence on survival, reproduction, and population size of mountain sheep (e.g. Douglas and Leslie 1986, Portier et al.1998). In the case of Dall sheep in Yukon and Alaska, poor lamb survival and recruitment were recorded during cold winters with high snowfall (Burles et al. 1984, Heimer and Watson 1984). Warmer and drier weather during summer was positively correlated with higher lamb production during the following season (Dry Creek, Alaska; Heimer and Watson 1986), and Hoefs (1984) demonstrated significant correlations between summer forage production on winter ranges, lamb survival during the following winter, and lamb production the following spring. Barichello and Carey (1988) concluded that winter snow conditions may play an important role in dynamics of sheep in the central Yukon based on observations of poor survival and reproduction following deep snows in winter 1982-83. While the impacts of particularly severe seasons are usually evident, it is often difficult to determine the longer-term effects of climate variation on mountain sheep populations because suitable census data are not available.

In addition to affecting lamb production and survival, climatic variability also has a significant influence on growth and condition of sheep. Ram horn growth is a potentially significant indicator of condition in sheep and goats (Geist 1971, Picton 1994, Festa-Bianchet et al. 1997, Côté et al. 1998, Picard et al. 1999), and horn growth has been used as a measure of response to climate, stress (measured as fluctuating asymmetry), and population bottlenecks (loss of genetic variability) (Picton 1994). There is also direct evidence that horn growth is limited by the availability of resources. In the Yukon, Hoefs and Nowlan (1997) demonstrated an almost two-fold difference in horn growth between captive and wild Dall sheep, indicating that resource availability plays a significant role in patterns of horn growth.

Growth of sheep horns provide a detailed proxy record for quantifying the effects of climatic variability on sheep, as the annual increment in horn size is a reflection of integrated climatic conditions influencing forage availability. In this study we examined patterns of horn growth of Dall sheep rams harvested in the southwest Yukon. Variability in patterns of growth are interpreted in relation to climatic variability on conditions in alpine sheep range, and we discuss potential underlying causes and long-term consequences of cohort variation in horn growth in this population.

STUDY AREA

The study area was located in the Ruby Ranges, southwest Yukon. The Ruby Range Mountains are located along the southwestern margin of the central Yukon Plateau, and they formed part of a southern arm of the intermittently ice-free Beringian land mass during the last glaciation (Hughes et al. 1968). This range consists of older, rolling mountains with generally continuous alpine meadows and discrete boulder fields (Oswald and Senyk 1977). These ranges are vegetated by characteristic alpine meadow species, have a short growing season (60-90 days), and low nutrient soils typical of alpine soils in general (Price 1971, McIntire 1999). Most of this area lies in the precipitation shadow of the St. Elias Mountains, and treeline occurs at about 1,200 m. In the valley bottom, average annual precipitation is 190-285 mm and average annual temperature is –4º C (Environment Canada, Burwash Landing meteorological station). Within the annual census area (part of the entire management zone), the sheep population has declined from approximately 900 adults (rams and ewes) in the early 1980s, to only about 600 adults by 1999, however the causes of this decline are not known (YTG, unpublished data). Harvest has remained relatively constant during this period. There is some preliminary evidence that available habitat may be declining (Weir and Hik 2001).

METHODS

Horn measurements

Measurements of Dall ram horn growth were collected from 1974 to1999 as part of annual harvest assessment in the southwest Yukon. These data include a total of 2481 individuals, however year of birth was known for only 1332. Of this sample, the number of individuals in each cohort ranged from 30 to186 individuals for year classes born between 1969 and 1992 (mean = 79 individuals). The age of each ram was determined by counting annual growth segments (Geist 1966, Hemming 1969). The length of annual growth segments were measured using a flexible tape measure placed along the frontal surface of the longer horn, and the lengths of all annual segments determined. The basal circumference of each annual segment was also measured. Measurements were made by conservation officers and biologists using standard methodology (Merchant et al. 1982, Barichello and Hoefs 1984).

Indices of Horn Size

Horn growth was calculated from linear measurements of annular length and circumference that were used to estimate horn segment volume. Volume of horn tips (age 1) were estimated as a cone ($V = \pi r^2 h/3$), while subsequent annual increments were estimated as conical fustra (Heimer and Smith 1975), such that Volume = $1/3 \pi h(R^2+Rr+r^2)$, where h is the estimated height and R and r are the respective base radii of the annual fustrum. Although horn tips were often broken or worn, resulting in inaccurate measurements (Hoefs and Nette 1982), the contribution of first year growth to the total horn volume of 8-year-old rams was less than 1%. Estimated volumes were adjusted using the correction factor of 0.544 ± 0.0033 (1 S.D.) calculated by Heimer and Smith (1975) in order to derive an estimate of true horn volume. A third estimate of horn growth, surface area estimated as annular circumference multiplied by the length of the annual increment (Picton 1994), was also calculated. It was highly correlated with volume ($r^2 > 0.95$, $p < 0.05$) and we did not consider it further.

Horn volume was used in subsequent analyses of cohort growth differences because it provides a better approximation of the actual amount of horn tissue laid down each year than segment length or diameter. However, we include a summary of patterns of increase in length for comparison with volume increases. We focused our analysis of cumulative horn volume at age 8 because approximately 85% of all rams can be legally harvested at this age (Barichello and Carey 1990). Sample sizes for older rams decrease significantly. We have considered 8-year-old animals as reaching maturity. This criterion is also consistent with behavioural observations of wild sheep, including studies by Geist (1971) and Heimer and Watson (1986). Statistical analyses were based on estimates of true horn volume and conducted using SPSS v.10. Results are presented as means $\pm$ 1 S.E.M., unless otherwise indicated.

RESULTS

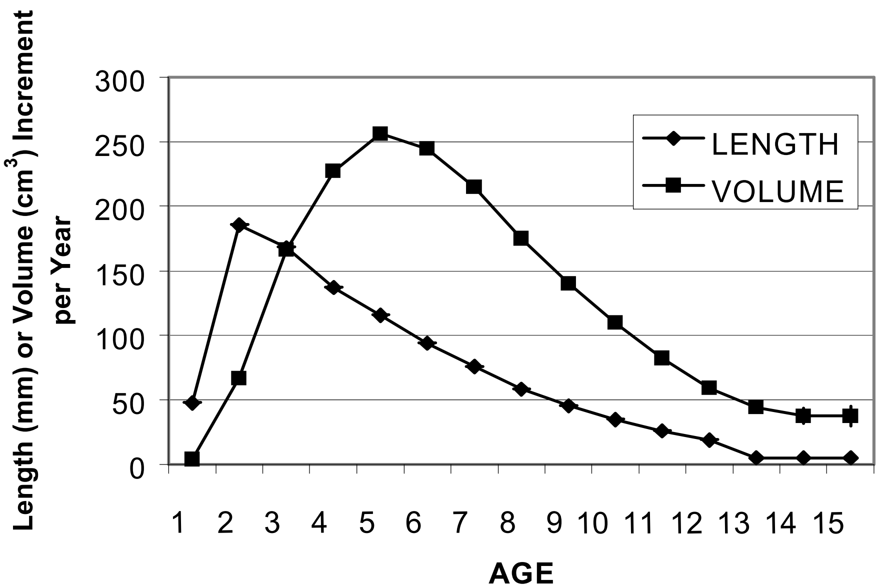
Patterns of horn growth

The pattern of horn growth exhibited by rams is consistent with the hypothesis that rapid acquisition of large horns is an important mating success strategy (Geist 1971). However, the apparent pattern of growth depends on how horn growth is characterized (Fig. 1). In terms of annual growth, maximum increments in horn length occur at a younger age than maximal estimates of horn volume (Fig 1A). Consequently the overall correlation between annual length and annual volume was low (linear regression: $r^2=0.121$, $p=0.268$). Annual increments of horn volume follow a quadratic pattern with maximum growth occurring during years 4 to 7, whereas annual increments in horn length decline after age 2. These patterns are very similar to those described by Heimer and Smith (1975). In the first year, horn growth is minimal, averaging about 7 cm^3 compared to 70 cm^3 in the following year. Cumulative length and volume (Fig. 1B) tend to reach a maximum between ages 8 and 10, and these cumulative measures are highly correlated (linear regression: $r^2 = 0.928$, $p<0.0001$). At age 8, the overall mean estimated horn volume of rams from all cohorts was 1298 ± 7 cm^3, while mean horn length was 826 ± 2 mm.

Cohort Variation in Horn Growth

Cohorts from 1969 to 1992 demonstrated significant variability in cumulative horn volume at 8 years (Fig. 2: ANOVA: $F_{23,1308} = 4.105$, $p < 0.0001$). Individual cohorts had horn volumes at 8 years that were up to 10% greater or less than the long-term mean volume (1298 cm^3). Horn length was also significantly different among cohorts during this 24-year period (Fig. 2: ANOVA: $F_{23,1317} = 2.864$, $p < 0.0001$), however the pattern was less variable, particularly during the 1980s. There was a significant correlation between horn volume and horn length at 8 years (linear regression: $r^2=0.463$, $p<0.0001$), indicating that both measures are showing similar patterns. However, horn volume is a more appropriate measure to use when analyzing cohort and annual variation.

A.



B.

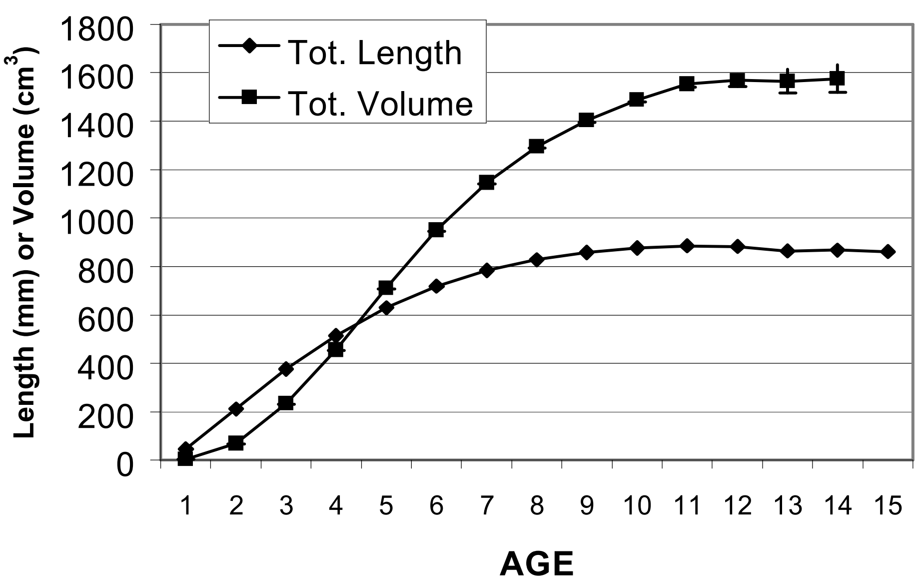


Fig. 1. (A) Annual increments and (B) cumulative increments of horn growth of Dall sheep rams measured as either length or volume (mean $\pm$ SEM). Sample sizes for each age group (1 through 15) are 1472, 2398, 2436, 2060, 2048, 1987, 1791, 1457, 1077, 664, 335, 135, 49,12 and 7, respectively.

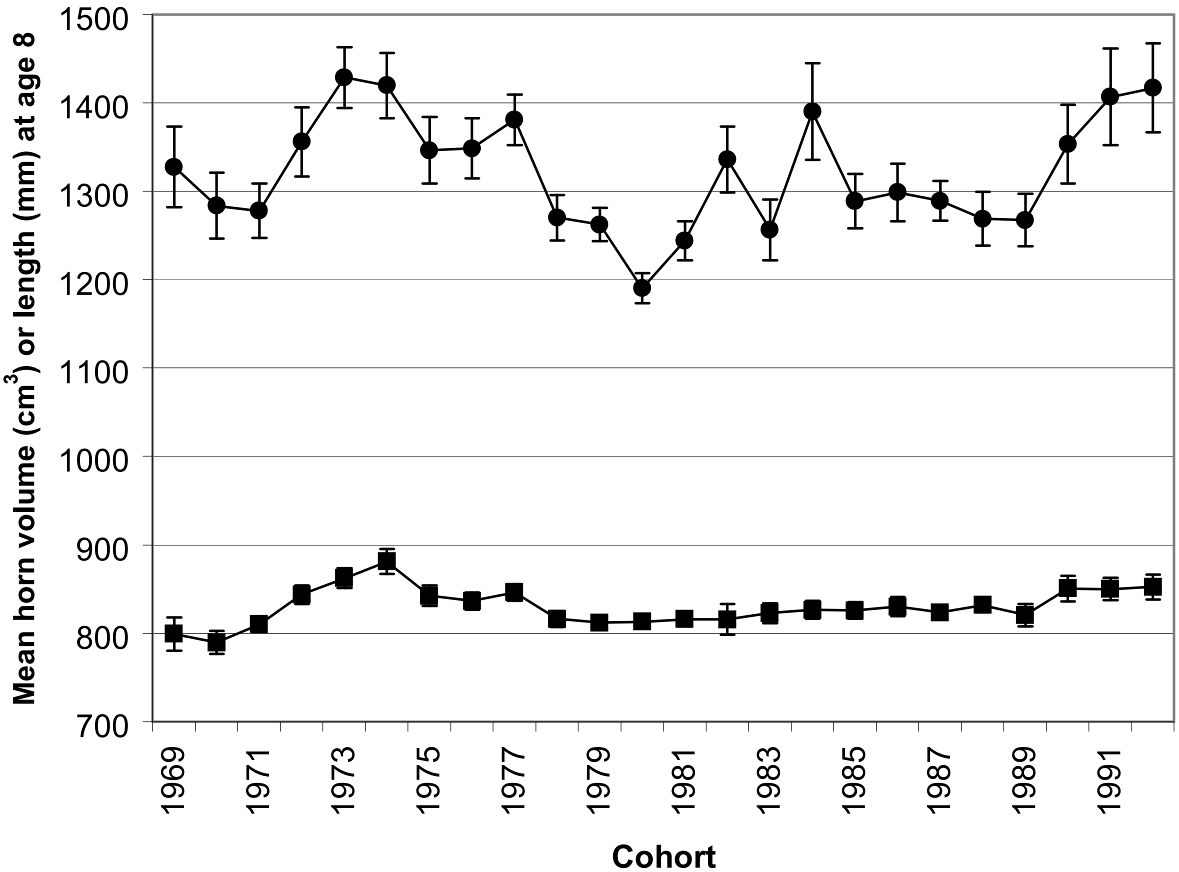
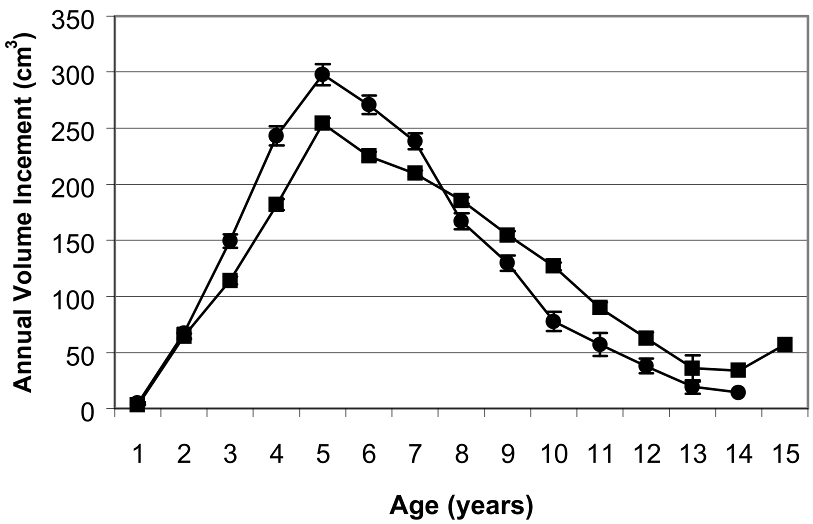


Fig. 2. Variation in horn volume (circles) and length (squares) of Dall sheep rams at age 8 for each cohort from 1969 to 1992 (mean $\pm$ SEM). Samples sizes are 11, 31, 53, 52, 52, 25, 32, 43, 57, 90, 131, 146, 78, 41, 46, 67, 59, 59, 89, 60, 44, 37, 19, and 10 for cohorts 1969 to 1992 respectively.

The greatest difference in horn volume at 8 years was between cohorts born in 1973 and 1980. Mean horn volume for rams in these two cohorts were significantly different (Tukey HSD test; $p<0.0001$) by almost 250 cm^3 (Fig. 2). This large difference at 8 years can be largely accounted for by age-specific differences in horn growth. The 1973 cohort experienced significantly greater increases in volume during years 3 to 7 than the 1980 cohort, however, after the eighth year this pattern was reversed (Fig. 3A). Nevertheless, since annual increments decrease after age 5 (Fig. 1A), rams surviving beyond age 8 years in the 1973 cohort typically had larger horns than older rams from the 1980 cohort. For instance, at age 13 horn volume for the 1973 cohort was 1760 ± 175 cm^3 (N=2) compared to 1707 ± 99 cm^3 (N=3) for the 1980 cohort, although the difference was no longer statistically significant (Fig. 3A). However, very few animals survive to this age in the region (Hoefs and Cowan 1979). Horn length also shows a similar overall pattern (Fig. 3B), such that annual increases in horn length for 3- and 4-year-old rams are significantly less for the 1980 cohort than the 1973 cohort, and there is little opportunity to 'catch-up' later in life.

A.



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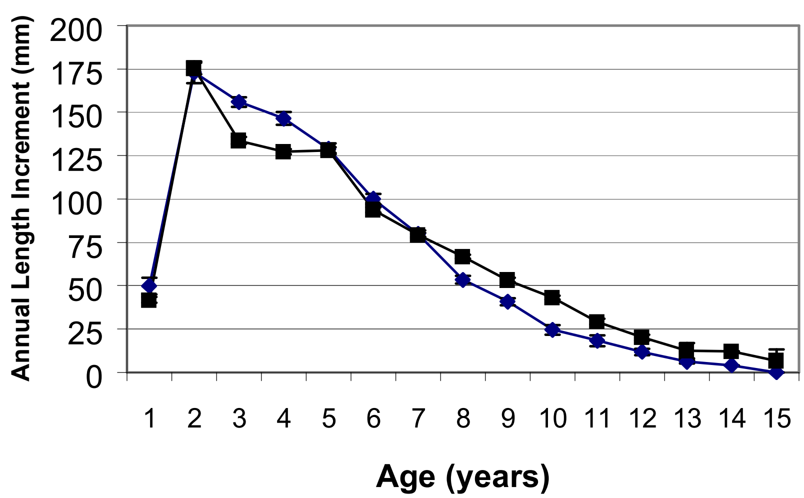

Fig. 3. Age specific differences in patterns of horn development and growth for Dall sheep rams born in 1973 (circles) and 1980 (squares) based on increments of (A) volume or (B) length.

To examine the long-term pattern of cohort variation in horn growth, deviations from the estimated overall (1969-1999) mean horn volume at each age were calculated for each age class in each year as an index of annual variation in horn growth (Fig. 4). These results clearly show periodic variation in growth that is strikingly consistent among cohorts and age-classes over the 30-year period of these records. In some years all individuals, regardless of age class or cohort have above-average growth, and in other years all individuals have below-average growth. A serial autocorrelation of this short time series identified the strongest periodicity for intervals of 10-years. Although there is some variability between age classes and cohorts (see Fig.4), the overall pattern is highly significant.

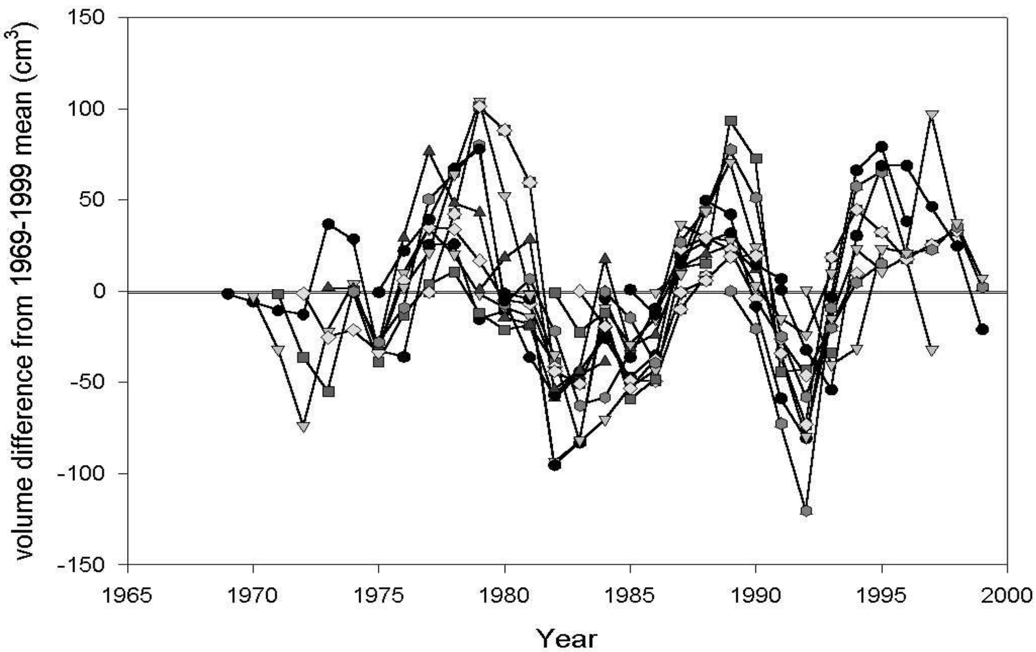

Fig. 4. Patterns of interannual variation in the horn growth (volume as cm^3) of individuals of each age class and cohort (1969-1999). Values are calculated as the difference between the annual and long-term mean values for each age/cohort class. Individual symbols and lines follow the difference in horn volume through each age class for each cohort, therefore the points in a given year indicate the deviation for all age classes of all cohorts living during that year.

Effect of Conditions in Birth Year on Horn Volume at Maturity

The results displayed in Fig. 4 strongly support a hypothesis that cohort variation in horn growth is periodic, with a frequency of approximately 10 years. In light of the patterns of age-specific annual growth rates described in Fig. 1, this periodic pattern raises the possibility that certain cohorts may experience better or poorer conditions for growth in a manner that is highly predictable, given the average life-span of rams in this population.

We defined a poor season as one that was characterized by below-average growth of all individuals in all cohorts and a good season as one during which horn growth was above-average for all rams, based on the deviations shown in Fig. 4. The cumulative differences between growth of all age classes in a given year and the long-term mean for each age class provided an index of values that indicate above- or below-average conditions. When these indices of conditions in a birth year are used to predict horn volume at age eight, the results show, surprisingly, that rams born in poor horn growth years will eventually have the largest horns at 8 years (Fig. 5).

Conversely, males born during relatively good years are likely to experience poor growth during years of maximum horn accretion, and therefore have smaller horns at 8 years. For example, rams born during one of the worst horn growth summers on record (1992) were among the larger horned cohorts at 8 years (see Fig. 2). This relationship (Fig. 5) is only marginally significant (linear regression: $r^2=0.122$, $p=0.101$), but the biological implications for hunters, outfitters, and managers are not trivial.

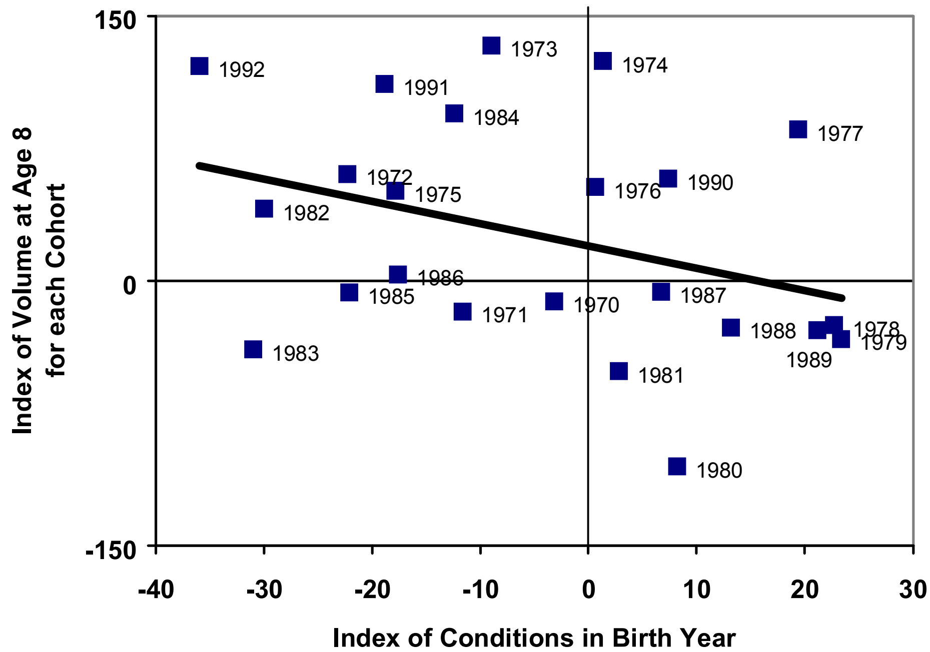

Fig. 5. Relationship between index of conditions in birth year and index of horn volume at age 8 for each cohort from 1970 to 1992. Indices are based on cumulative differences in horn growth from long-term mean values for each age/cohort group. Negative values indicate below-average conditions in the year of birth (x-axis), or below-average horn volume at age 8 (y-axis).

DISCUSSION

Overall, patterns of horn growth of Dall sheep rams over 30 years indicate strong interannual variation with a periodicity of approximately 10 years. Depending on the year of birth, individual rams will have different trajectories of horn growth during the first decade of life. These strong cohort effects in horn growth were also detected in an earlier examination of horn growth data from this region (Bunnell 1978, Mindek 1989), and these authors suggested that cohort effects on early horn growth were compensated for by better growth in later years. While this may be true for animals that live for at least 10-12 years, relatively few animals reach this age in the Yukon. In alpine ibex, Toigo et al. (1999) observed that environmental effects during the first year influenced horn growth of males, and that these animals were unable to compensate for poor growth during later years, emphasizing the importance of cohort effects in this population.

Another possible explanation for our results is that horn growth is dependent on population density as suggested by Geist (1971). Heimer and Smith (1975) also speculated that density-dependent nutrition might influence population quality for Dall sheep, however this hypothesis was refuted in subsequent studies (see Heimer and Watson 1986, Heimer 1999). The density of the sheep population in the Ruby Range during the past 30 years is probably well below historical numbers (J. Johnson, personal communication), and has declined since 1980 (Carey et al. unpublished data). Although cohort-related effects may be related to density in some populations of bighorn sheep (*Ovis canadensis*), Jorgenson et al. (1998) showed that population density only influenced horn growth of young rams

(<4 years age). During this time males are still associated with nursery bands, and higher intraspecific competition for resources may limit horn growth. The effects of density disappeared once rams joined all-male groups. In our analyses, Dall sheep rams of all age classes showed correlated changes in horn growth (Fig. 4), indicating that changes in relative density of nursery herds associated with interannual variability in reproductive success could not explain the periodic patterns of growth in the southwest Yukon.

The basis for the observed periodic variation in ram horn growth appears to be mediated through the influence of annual climatic conditions on primary productivity of alpine habitats utilized by sheep for forage. Hoefs and Brink (1978) found that precipitation during the summer growing season was correlated with primary productivity of sheep range. Summer productivity was also directly correlated with reproduction during the following season (Hoefs 1984). In our study area in the Ruby Range the relationship between ewe: lamb ratios and an index of summer weather conditions (the deviation of June to August minimum temperature from average minimum temperature, multiplied by summer precipitation), was positive and significant (linear regression: $r^2 = 0.642$, $p=0.002$, $N=11$; Carey et al., unpublished data). Several authors (e.g. Hoefs and Brink 1978, Mindek 1989) have attempted to describe particular environmental conditions associated with poor growth, but this analysis is difficult at present without knowing more about how variation in environmental conditions influence vegetation productivity (D. Hik, unpublished data). However, several recent studies have demonstrated that large-scale weather variation can influence synchronization and periodicity of population dynamics of large mammals including Soay sheep (*Ovis aries;* Grenfell et al. 1998, Milner et al. 1999) and red deer (*Cervus elaphus;* Forchhammer et al. 1998).

In the southwest Yukon, the deviation from the long-term mean volume in ram horn growth is also broadly synchronized and correlated with the cycle in snowshoe hare (*Lepus americanus*) numbers from the adjacent boreal forest (see Krebs et al. 2001). A bivariate spectral analysis of these two time series found that periodicities of 11 years were strongest, and that cross-correlation analysis indicated that the strongest relationship occurred with a lag of –2 years ($r = 0.5741$, $p < 0.05$; Hik and Carey, unpublished data). This relationship essentially implies that the periodic pattern observed in horn growth precedes the hare cycle by two years, consistent with the suggestion that growth or condition is a more sensitive indicator of environmental conditions than adult survival, which may remain high even in years when individuals are in poor condition (Hik 1995). More significantly, the periodicity of horn growth and the correlation with the snowshoe hare cycle provides support for the hypothesis that there is a general underlying climate-mediated influence on herbivore growth and survival in this northern region (Sinclair et al. 1993).

In the southwest Yukon the observed periodicity in horn growth may provide a strong terrestrial signal of inter-decadal climatic variability associated with large-scale oceanic phenomena such as the Pacific Decadal Oscillation, and these periodic anomalies in atmospheric flow over the Pacific Ocean may have profound consequences for the weather of North America, particularly during winter (Bond and Harrison 2000). The length of the sunspot cycle also correlates well with indicators of terrestrial climate in the Northern Hemisphere (Friis-Christensen and Lassen 1991, Fligge et al. 1999), although inclusion of other factors such as volcanic dust and greenhouse gases improves the relationship (e.g. D'Arrigo et al. 1999). While the direct link between climate cycles and sunspots is still uncertain (Waple 1999), there is a clear need to examine specific mechanisms that link climate, vegetation dynamics, habitat quality and productivity, and the demography and growth of terrestrial wildlife population in the Yukon.

Although several attempts have been made to link weather directly to observed variation in horn growth, this is difficult without knowing details of what factors influence plant productivity. Mysterud et al. (2000) have similarly discussed the need to carefully evaluate impacts of specific local weather conditions on forage productivity before firm conclusions can be drawn between climatic periodicity and dynamics of northern ungulates. Ongoing studies in the Ruby Range suggest that net annual primary productivity of alpine meadows is most strongly influenced by the timing of snow-melt, however summer temperature and precipitation are also important (D. Hik, unpublished data). Winter conditions may also restrict access to forage on winter range (Goodson et al. 1991), which could influence the correlation between summer productivity and horn growth.

Several attempts have been made to correlate specific changes in temperature and precipitation with primary productivity (e.g. Hoefs and Brink 1978, Mindek 1989), however there is no clear relationship and horn growth is probably a better bio-indicator of average conditions in this region than generalized weather records. As well, strong temperature inversions occur in Yukon mountains (Burn 1994), and therefore climate records from the valley bottom may not be representative of climate at higher elevations, particularly in winter (D. Hik, unpublished data). While the instrumental climate record is probably too short to detect clear patterns, a significant 11-year periodicity has been observed for both precipitation and temperature based on a 250-year time series analysis of ice-core records (1736-1986) from the summit of Mt. Logan, only 100 km west of the Ruby Range study area (Holdsworth et al. 1992).

MANAGEMENT IMPLICATIONS

While the prevailing wisdom is that northern sheep populations are self-regulatory and thus tend to manage themselves (Geist 1971, Hoefs 1984), the results of these analyses emphasize several important management implications for the southwest Yukon. First, there is a distinct cohort effect on horn growth that is broadly predictable because it is correlated with larger-scale climate patterns that operate on decadal and multi-decadal scales, even though the precise ecological mechanisms are unknown. Geist (1971) suggested that variation in horn growth in North American wild sheep was an indication of the quality of a population, such that more rapid horn growth and more massive horns at any given age would be characteristic of high quality populations. In the case of Dall sheep in the southwest Yukon, periodic climate-mediated effects appear to influence horn growth of rams in specific cohorts. Therefore, selective removal of large-horned rams by hunters should have no influence on the genetic quality of a population, or on the potential of the population to produce more rams with fast-growing horns.

Second, our results suggest that large rams will only be produced periodically in the Ruby Range populations. The largest rams will come from cohorts born during poor summers, further confounding the potential for producing many large rams at any time in this population because there is lower lamb survival during poor summers. These rams may in fact be harvested at a younger age because they experience more rapid horn growth (Fig. 3). By age 12 or 13 years there is very little difference in the size of horns of individuals born in good or poor seasons.

Finally, we suggest that other jurisdictions consider programs for measuring annual horn growth of harvested rams. This detailed information may allow sheep horns to serve as valuable bioindicators of interannual variation in the quality of sheep habitat. The underlying causes of this variability may not be easily explained, but without measurements of annual growth it is impossible to even ask these questions. Estimates of volume based on measurements of length and basal circumference provide superior information than measurements of length alone.

ACKNOWLEDGMENTS

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PARASITE BIODIVERSITY, DEVELOPMENT, AND TRANSMISSION: AN INTEGRATIVE MODEL FOR MONITORING CLIMATE CHANGE AT NORTHERN LATITUDES

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Abstract: The survival, development, and transmission of helminth parasites is intimately linked to environmental conditions. It follows that a changing global climate, particularly global warming, will profoundly influence the abundance of parasitic organisms in wildlife, ultimately exerting an effect on the abundance and distribution of various host species. Such issues may be exacerbated in the Arctic where the biotic response to global warming is predicted to be profound. Despite the potential role that parasites play in host population dynamics, there is very limited published information on the parasite fauna of arctic mammals, particularly ruminants. Qualitative and quantitative baseline knowledge of the biodiversity, geographic distribution, and host associations for the parasite fauna characteristic in arctic mammals is important for predicting and monitoring the effect of climate change on the host-parasite systems in northern environments. Once understood, these systems, which can be indicators of the variation in abiotic processes that are determinants of biodiversity over prolonged periods, may be used in a more comprehensive model for monitoring the potential impact and response to climate change. Recent research on a remarkable lungworm (*Umingmakstrongylus pallikuukensis*) in muskoxen (*Ovibos moschatus*) has resulted in a model for assessing biotic response to warming. This multifaceted model is based on the concept that seasonal limits on transmission and the potential for amplification of parasite populations over time are intimately linked to temperature and development rates larval parasites. Parameters integrated in the model, in part validated by field studies, include threshold temperatures and degree-day requirements for parasite development in the external environment, the behaviour of the intermediate hosts, and soil surface temperatures. This model can be used both to monitor parasite development in the environment as well as to predict parasite development in other environments or geographic locations. In addition the model could be adapted and applied to other members of the Protostrongylidae in other hosts (e.g., Dall's sheep and mountain goats) in the Arctic and Subarctic to increase our knowledge of these host-parasite systems and the biotic and abiotic controls on their distribution.

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HUNTER SATISFACTION WITH TROPHY DALL SHEEP MANAGEMENT IN THE TOK MANAGEMENT AREA, ALASKA

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Abstract: The Tok Management Area (TMA) was created in 1974 to provide a limited number of Dall sheep (*Ovis dalli*) hunters the opportunity to harvest large-horned, trophy rams. The chance of obtaining 1 of the 120 TMA drawing permits ranged from 4% to12%. Hunter satisfaction with the TMA was not evaluated objectively nor was the willingness to accept alternative management options determined. We conducted a mail survey of randomly selected TMA applicants to assess satisfaction with trophy Dall sheep management goals and objectives and the hunt structure of the TMA. Over 90% of respondents supported the present TMA management objectives for maintaining a limited number of drawing permits, limiting harvest to benefit trophy ram management, and preventing hunter crowding. Less support existed (78%) for the current objective of maintaining the proportion of harvested rams with ≥40-inch (1016 mm) horns at 7-10%. Our results indicated there were 4 distinct philosophies among respondents regarding how the TMA should be managed. Differences were due to how respondents defined a trophy ram, sheep hunting experience, and what was considered acceptable hunter opportunity. We describe management options that could satisfy 3 of the 4 groups (97% of the respondents). In the case of the TMA, using the hunt's popularity to measure acceptance may have perpetuated management that did not meet the original intent of a trophy sheep area or best fit sheep population and hunter use trends. We recommend that prior to developing other trophy or restrictive hunt areas, managers and the public work together to objectively define goals and objectives, so future management changes are justified.

Key words: Dall sheep, *Ovis dalli*, Alaska, Tok Management Area, trophy sheep management, hunter crowding management, public satisfaction, questionnaire.

The Tok Management Area (TMA) was created in 1974 with the goal of providing Dall sheep hunters the opportunity to harvest trophy rams in an uncrowded setting. In comparing horn growth qualities of Dall sheep rams inhabiting 7 mountain ranges in Alaska, rams in the TMA exhibit the second greatest horn length and the fourth greatest horn mass qualities (Heimer and Smith 1975). The TMA is the only sheep hunting area in Alaska specifically established for trophy ram management and is the most sought after sheep hunt permit in Alaska. Each year 2,300-2,500 hunters apply for 120 permits to hunt in the TMA.

Four objectives have guided TMA management since its inception:

1. Maintain a population capable of supporting an annual harvest of 30-45 rams;
2. Maintain a mean horn length of 36-37 inches (914-940 mm) among harvested rams and a mean age of 8-9 years;
3. Maintain the proportion of harvested rams with ≥ 40-inch (1016 mm) horns at 7-10%; and

4. Prevent unacceptable increases in hunter concentration and maintain the existing aesthetically pleasing qualities associated with sheep hunting in the TMA.

These objectives are met by controlling the number of sheep hunters through a drawing permit system. This system was designed to limit annual harvest and allow some rams to attain larger horn sizes. During 1974-1999, 120 permits were issued each year. Hunter satisfaction with the system was never measured objectively but hunter success, in terms of proportion of harvested rams with horns ≥ 40 inches (1016 mm, 7%-19% of the annual harvest, 1986-1999) indicated the system allowed rams to reach maximum horn size and hunters to be selective in taking a ram.

From 1995 to1999, participation rate increased by 29%. An increasing number of hunter complaints and higher annual harvests prompted us to re-examine the TMA goals and objectives by assessing hunter satisfaction. We plan to use results of this survey to help design future TMA management.

Our goals were to develop a questionnaire assessing characteristics of hunters applying for the TMA, what their attraction to the area was, and what management direction is most acceptable to them. In a cover letter for the questionnaire we included sheep population and harvest data not known by most hunters who have applied for a TMA permit.

METHODS

Survey design

We developed a survey consisting of 45 questions addressing 4 areas: hunter profiles, management options, trophy ram definition, and conditions affecting hunter crowding and enjoyment. The respondent profile section focused on sheep hunting experience in Alaska and the TMA. We wanted to evaluate if sheep hunting experience or past success might affect respondents' views. For example, a hunter who had previously taken a large ram (horns ≥40 inches, 1016 mm) may have a different view on trophy management than someone who had taken a smaller ram (≤ 40 inch, 1016 mm) or no ram at all.

Questionnaire recipients were asked to respond on a Likert scale (Strongly Agree, Agree, Neutral, Disagree and Strongly Disagree) to questions concerning support for current management objectives, trophy ram definitions, optimal hunting conditions, and management options. Hunters were also asked on a Likert scale (Strongly Enhances, Enhances, Neutral, Detracts, and Strongly Detracts) which conditions affect their enjoyment of the hunt. The conditions evaluated were harvest success, the availability of rams with different horn sizes, and the effects of hunter crowding.

Recipients were asked to rank 5 trophy management options and 6 hunter crowding management options from most supportable to least supportable. Options ranged from increasing hunting opportunity from current levels with little regard for trophy ram management and hunter crowding to reducing hunter opportunity in order to increase the number of trophy rams. Hunters could also choose management options currently in use.

We asked hunters to explain in their own words what constitutes a trophy ram and how they would manage the TMA. Responses were hand tabulated and used to index respondent understanding of survey questions and whether the survey covered the range of hunters' views and desires.

We mailed the survey to 575 hunters randomly chosen from all people who had applied for a TMA permit during 1995-1999. Expecting return rates for people who had never drawn a TMA permit to be less than those who had, the sample included 275 people who had been drawn and 300 people who had not. A second survey mailing was sent 2 weeks following the initial mail out. As a pretest for clarity and inherent biases, the survey was presented to 20 sheep hunters, 2 wildlife planners, 2 sheep biologists, and 2 non-hunters. Their suggestions were incorporated into the survey.

Statistical analyses

Data were analyzed using the SAS software package (SAS 1988). The FREQ procedure was used to generate frequency and cross tabulation tables. Statistical tests used the Pearson chi-square statistic for tables when the majority of cells had expected counts ≥ 5 and the Fisher exact test for smaller samples. A significance level of p=0.10 was used for testing. Because TMA permit applicants were drawn at a different rate than permit recipients responses were weighted using the inverse of the probability of being selected to receive the questionnaire. Weighting was carried out in all analyses.

Multiple comparisons based on ranking and selection was used to determine which management options were significantly different (Hsu 1996). Discriminant analysis was used to confirm groupings of philosophies and attitudes. The DISCRIM procedure was used with prior probabilities of group membership set proportional to the sample sizes. Various groupings of questions were created for use in the discriminant analysis and classification probabilities were used to judge which sets of questions provided the best confirmation. Question groups used were: current management objectives, hunter enjoyment, hunter crowding, trophy sheep hunting, crowding-management objectives, and trophy management objectives. Selection of question groups in the discriminant analysis also provided assistance labeling groups.

RESULTS

Respondent profile

Of 575 surveys sent, 383 were returned and 298 were used in analyses. Eighty-five of the surveys were unusable because they were returned undeliverable, incomplete, or late. The usable return rate was 61%.

Recipients who had drawn a TMA permit responded at a higher rate (70%), than those who had never drawn a permit (34%). Respondents who had drawn a permit comprised 64% of the sample and respondents who had never drawn comprised 36% of the sample. Of respondents who had drawn a permit, 91% had hunted the TMA and had a 55% harvest success rate. Mean participation and harvest success rates in the TMA during 1995-1999 were 84% and 51%, respectively. Ninety-six percent of respondents had hunted sheep in Alaska of which 80% had ≥3 years experience hunting sheep.

Recipients were asked the horn length of the largest ram they had killed in Alaska. Of 190 who responded to this question, 8% reported horn lengths ≤34 inches (864 mm), 56% reported horn lengths 34 to 38 inches (864-965 mm), and 36% reported horn lengths ≥38 inches (965 mm). Twenty percent of respondents reported taking a ram with horns ≥ 40 inches (1016 mm). Average horn size reported by respondents that harvested a ram in the TMA was 37.9 inches (963 mm). Based on mandatory reporting, mean horn length of all rams taken in the TMA during 1995-1999 was 36.5 inches (927 mm).

Management options

Over 90% of the respondents supported the present TMA management objectives for maintaining the drawing permit, limiting harvest to benefit trophy ram management, and preventing hunter crowding (Table 1). When asked about support of the current management objective using a specific range of horn sizes in the harvest as a measure of management success, 78% were in agreement (Table 1). There was no significant difference between respondents who had received a TMA permit and those who had not (*p*=0.245), between experienced and inexperienced hunters (p=0.864) or between hunters who had harvested a TMA ram and those who had not (p=0.615).

We asked 6 questions about possible management changes that would affect hunter opportunity, hunter crowding and trophy hunting (Table 2). There was no support for increasing permit numbers to allow more hunter opportunity (93% against) at the expense of hunter crowding or trophy ram production (91%). There was support (79% agree) for reducing permits if crowding became apparent. There was no preference for or against reducing permit numbers to restrict harvest and increase the number of rams with ≥40-inch (1016 mm) horns. Of 295 respondents, 43% agreed and 41% disagreed with this proposal. Respondents ranked potential options for trophy (5 alternatives) and crowd management (6 alternatives). For crowd management, maintaining the current hunt structure was preferred by most (85%) respondents ($p \leq 0.009$, Table 3). Support for no-change declined to 77% when respondents considered a range of trophy ram management options ($p \leq 0.001$, Table 4). Reducing permit numbers for either trophy management or hunter crowding became one of the least preferred options.

Multiple comparisons between trophy management options found 3 similar and 2 differing options (Table 5). Similar options include continuing the current hunt structure; maintaining 120 permits, subdividing the TMA, and periodically closing some areas to enhance trophy sheep; and subdividing and managing the TMA as separate areas. Reducing the number of permits to enhance ≥40-inch (1016 mm) rams and increasing the number of permits from 120 received lower preference. Maintaining the current hunt structure was chosen by most respondents (39%, $p< 0.01$) as their preferred choice.

Table 1. Ranking of support for current TMA management objectives, determined from responses of 298 TMA permit applicants.

Management Objective	% Strongly Agree (n)	% Moderately Agree (n)	% Neutral (n)	% Moderately Disagree (n)	% Strongly Disagree (n)
Remain drawing hunt	85.1 (251)	9.2 (27)	3.7 (11)	1.7 (5)	0.3 (1)
Maintain harvest below sustainable to benefit trophy ram management	66.0 (194)	23.5 (69)	5.1 (15)	3.1 (9)	2.4 (7)
Maintain 7-10% of harvested rams with horn length ≥40”	47.1 (138)	30.7 (90)	17.4 (51)	2.7 (8)	2.0 (6)
Manage for maximum opportunity to harvest and/or observe large-horned rams	69.5 (205)	20.7 (61)	5.1 (15)	2.0 (6)	2.7 (8)
Manage to prevent overcrowding	70.5 (208)	22.7 (67)	3.1 (9)	2.7 (8)	1.0 (3)

Table 2. Ranking of management options affecting opportunity, crowding and trophy ram production in the TMA, determined from responses of 298 TMA permit applicants.

Statement	% Strongly Agree (n)	% Moderately Agree (n)	% Neutral (n)	% Moderately Disagree (n)	% Strongly Disagree (n)
Increase # of permits	3.7 (11)	7.1 (21)	8.2 (24)	27.6 (81)	53.4 (157)
Allow more hunters regardless of effects on crowding	1.7 (5)	3.4 (10)	2.0 (6)	22.5 (66)	70.3 (206)
Allow more hunters regardless of effects on trophy ram management	2.0 (6)	3.7 (11)	3.1 (9)	24.1 (71)	67.1 (198)
Reduce # of permits if crowding becomes apparent	36.4 (106)	34.0 (99)	8.9 (26)	11.0 (32)	9.6 (28)
Reduce # of permits to increase number of rams with horns ≥40"	18.0 (53)	25.1 (74)	15.9 (47)	25.8 (76)	15.3 (45)
Do not reduce # of permits to reduce crowding	21.9 (64)	26.7 (78)	18.8 (55)	17.5 (51)	15.1 (44)

Table 3. Ranking of options for managing hunter crowding in the TMA, determined from responses of 298 TMA permit applicants.

Management option	Ranking[1] percentage (n)					
	1	2	3	4	5	6
Retain drawing permit but increase # of permits	4.1 (12)	5.5 (16)	9.3 (27)	16.6 (48)	37.2 (108)	27.2 (79)
Take TMA off drawing permit	2.7 (8)	1.4 (4)	2.4 (7)	6.2 (18)	14.4 (42)	72.9 (212)
Increase # of permits but maintain uncrowded hunting by dividing season each w/ its own permit	16.1 (47)	17.8 (52)	26.0 (76)	20.9 (61)	7.9 (23)	11.3 (33)
Make no change to current TMA hunt	39.4 (115)	21.9 (64)	23.6 (69)	7.9 (23)	3.1 (9)	4.1 (12)
Reduce # of permits	9.6 (28)	15.4 (45)	16.8 (49)	20.5 (60)	16.4 (48)	21.2 (62)
Maintain current # of permits and reduce crowding by subdividing TMA with each area having its own permit	26.4 (77)	25.3 (74)	18.5 (54)	8.9 (26)	6.2 (18)	14.7 (43)

[1] 1 being the option most supported and 6 being the option least supported

Table 4. Ranking of management options for trophy ram production in the TMA, determined from responses of 298 TMA permit applicants

Management option	Ranking[1] percentage (n)				
	1	2	3	4	5
Increase # of permits w/ no regard to effects on #'s of large-horned rams	2.4 (7)	2.4 (7)	2.4 (7)	4.5 (13)	87.8 (253)
Maintain current # of permits, subdivide TMA and manage each area to produce more large-horned rams	23.5 (67)	34.4 (98)	22.8 (65)	9.5 (27)	9.5 (27)
Maintain current # of permits; subdivide TMA and periodically close individual areas to hunting to produce more large-horned rams	22.5 (64)	23.2 (66)	34.0 (97)	10.5 (30)	9.8 (28)
Reduce # of permits to produce more large-horned rams	14.0 (40)	12.2 (35)	18.2 (52)	39.9 (114)	15.7 (45)
Make no changes to current TMA hunt	38.7 (111)	18.5 (53)	19.2 (55)	19.2 (55)	4.5 (13)

[1] 1 being the option most supported and 6 being the option least supported

Table 5. Ranking and selection of 5 possible management options that would affect trophy ram production in the TMA, determined from responses of 298 TMA permit applicants.

Management options	Sample mean	Standard error
Maintain current hunt structure	2.324[a1]	0.076
Maintain # of permits at 120, subdivide TMA and individually manage each area	2.478[a]	0.073
Maintain # of permits at 120, subdivide TMA and periodically close areas to enhance trophy ram production	2.618[a]	0.072
Reduce # of permits to enhance production of rams with horns ≥ 40"	3.308[b]	0.075
Increase # of permits	4.73[c]	0.049

[1]Same superscript letter indicates means did not differ ($p > 0.10$)

Hunter philosophies

Our analyses initially suggested there were 3 distinct philosophies among questionnaire respondents regarding how the area should be managed. Differences were due to how respondents defined a trophy ram, their sheep hunting experience, and what they considered acceptable hunter opportunity. We labeled the 3 groups "Contents", "Trophies", and "Opportunities".

The Contents was the largest group, (77% of respondents), and was most satisfied with the current trophy management strategy. This group was primarily interested in maintaining hunter opportunity without causing hunter crowding. The Trophies (20% of respondents) favored additional management to enhance trophy ram production. The Opportunities group (3% of respondents) desired increased opportunity regardless of the effects on abundance of trophy rams or overcrowding.

Discriminant analysis was carried out to confirm the Contents and Trophies groupings. We did not include the Opportunities group because it represented only 3% of respondents. Using trophy definition and trophy management questions, all members of the Contents were classified correctly. Eighty percent of the Trophies were classified correctly. We examined the 20% misclassified (3% of the total response) and concluded they were neither Trophies nor Contents, but a 4th group, which we then labeled "Purists". This group was most interested in protecting uncrowded hunting conditions and increasing harvest success rates in the TMA and was willing to reduce opportunity to do so.

Trophies and Contents differed statistically on preferred management options for both trophy and hunter management. Opportunities and Purists were excluded from group comparisons because group sizes were too small for valid chi-square analysis. For trophy management, Trophies preferred maintaining current permit numbers, subdividing the TMA and closing some of the areas as needed to enhance trophy ram production (p=0.014, 63% accept, 7% reject for Trophies, vs. 41% accept, 23% reject for Contents). Trophies supported reducing permits to increase the number of rams with horns ≥40 inches while the Contents did not (p=0.001, 54% accept, 7% reject vs. 20% accept; 67% reject). Both groups agreed there should be areas in Alaska that are managed to enhance production of large-horned rams but the Trophies showed stronger agreement than the Contents (p=0.015, 91% accept, 6% reject vs. 81% accept, 12% reject). Correspondingly, although both groups agreed areas should be managed to increase the chances of harvesting a Boone and Crockett ram, Trophies showed more support than Contents (p=0.001, 84% agree, 5% reject vs. 56% agree, 25% reject).

These 2 groups also differed in management philosophies regarding reduction of permits to lessen hunter crowding. Trophies supported reducing the permit numbers (p=0.001, 59% accept, 14% reject) while Contents tended to reject the idea (17% accept, 42% reject).

Trophy Definition

Overall, 72% of respondents agreed that any legal (i.e. full curl) ram was a trophy (Table 6). However, when asked whether all full curl rams were trophies, 42% of respondents agreed that only some full curl rams were trophies compared to 46% who felt that all full curl rams were trophies. Narrative answers from 24% of respondents indicated subjective factors such as how hard the hunter worked, the scenery, solitude, and horn uniqueness in combination with horn size defined a trophy ram. The Trophies group also did not accept that any legal ram was a trophy (p=0.051), because horn size was an important component of their definition.

Defining a trophy ram using quantifiable standards (horn lengths of ≥ 40 inches (1016 mm) and rams scoring ≥170 Boone and Crockett points) was rejected by 56% and 61% of all respondents, for length and score respectively. Respondents who had not harvested a TMA ram were more likely to agree that only rams with horns ≥ 40 inches are a trophy (p=0.007, 37% agree, 45% disagree vs. 27% agree, 66% disagree). Respondents who had not harvested a TMA ram were also more likely to agree with using ≥170 Boone and Crockett points to define a trophy ram (p=0.009, 21% agree, 49% disagree vs.12% agree, 75% disagree). Thirty-three percent of respondents who defined a trophy ram in their own words used length of horn. Of these respondents, a trophy was defined as a ram with horns ≥ 40, ≥38, and ≥36 inches by 54, 28, and 18%, respectively.

Table 6. Definition of trophy ram, determined from responses of 298 TMA permit applicants.

Definition	% Strongly Agree (n)	% Moderately Agree (n)	% Neutral (n)	% Moderately Disagree (n)	% Strongly Disagree (n)
Any legal ram is a trophy	33.3 (98)	38.8 (114)	10.2 (30)	8.2 (24)	9.5 (28)
Only rams with horns ≥40" are trophies	11.6 (34)	19.1 (56)	13.7 (40)	25.6 (75)	30.0 (88)
Only rams that meet Boone & Crockett qualifications are trophies	5.1 (15)	12.3 (36)	21.6 (63)	21.6 (63)	39.4 (115)
Not all full curl rams are trophies	12.2 (36)	29.6 (87)	12.2 (36)	22.4 (66)	23.5 (69)

Hunter Enjoyment

The 3 factors respondents identified as enhancing hunting enjoyment in the TMA were: not seeing other hunters, not hearing other hunters, and taking a ≥40 inch (1016 mm) ram ($p=0.001$, 89% enhance, Table 7). Seeing many sheep but few legal rams detracted from the hunt experience for 60% of respondents. Observing few rams with horns ≥ 40 inches (1016 mm) but many legal rams diminished the quality of the hunt experience for 28% of respondents but 51% of respondents reported this condition would enhance their hunt. Failure to harvest a ram detracted from the experience for 51% of the respondents but 47% said it had no effect.

Table 7. Ranking of conditions that affect sheep hunting experience, determined from responses of 298 TMA permit applicants.

Condition	% Strongly Detracts (n)	% Moderately Detracts (n)	% No Effect (n)	% Moderately Enhances (n)	% Strongly Enhances (n)
Seeing many sheep but few legal rams	22.9 (67)	37.2 (109)	160 (47)	21.2 (62)	2.7 (8)
See many legal rams but few or no rams with horns ≥40"	5.2 (15)	22.3 (65)	21.6 (63)	34.0 (99)	16.8 (49)
Taking a ram with horns ≥40"	0.7 (2)	1.7 (7)	8.3 (24)	12.8 (37)	76.4 (220)
Not harvesting a ram	11.8 (34)	39.4 (114)	47.4 (137)	0.3 (1)	1.0 (3)
Hearing other hunters during hunt	41.4 (122)	48.1 (128)	9.8 (29)	0.3 (1)	0.3 (1)
Seeing other hunters during hunt	46.1 (136)	43.7 (129)	9.8 (29)	0.3 (1)	---

Conditions affecting hunter enjoyment differed according to hunter experience, TMA experience, and harvest success. We found failure to harvest a ram lessened hunter enjoyment significantly more ($p=0.023$) for inexperienced hunters (63%) than experienced hunters (47%). Respondents harvesting a TMA ram were more satisfied seeing many legal rams but few ≥40 inches (1016 mm) ($p=0.017$) compared to non-harvesters.

Not harvesting a ram had little effect on hunt enjoyment for the Trophy group but detracted from the experience for Contents (p=0.013, Trophies: 39% detract, 60% no effect vs. Contents: 54% detract, 44% no effect). The Trophy group believed seeing many sheep but few legal rams detracted more from hunt quality than did the Contents group (p=0.015, Trophies: 71% detract, 15% enhance vs. Contents: 57% detract, 26% enhance). Negative effects of seeing many legal rams but few rams ≥ 40 inches (1016 mm) were greater for the Trophies than for the Contents (p=0.075, Trophies: 37% detract, 45% enhance vs. Contents: 25% detract; 52% enhance).

DISCUSSION

Since establishment of the TMA, public acceptance of our management strategy has been measured informally by the number of complaints received, number of proposals submitted by the public to change TMA regulations, and by the number of applicants for a TMA permit. Based on these criteria, the TMA and its management are well accepted by hunters. Most people who apply have done so for multiple years, some for over 20 years. Since 1974, Alaska Department of Fish and Game (ADF&G) has received few complaints. Most criticisms concerned hunter crowding and were received since 1995. From 1990-1999, there was only 1 proposal for change in TMA management and that was to increase opportunity for bow hunters. The Alaska Board of Game, after reviewing the intent of the TMA and public and agency comments, did not adopt this proposal into regulation.

Incorporating public views has become an important step in effective wildlife management. Ignoring these views discounts the strong interest of the public concerning wildlife and has led to political backlash. In Alaska, most exchange of information between the public and the ADF&G occurs in the Board of Game process. The Alaskan public has never been shy in expressing views concerning wildlife management.

There is an important difference between the TMA and most other areas in Alaska when it comes to incorporating public views in management decisions. Because the TMA is managed by a permit that is difficult to obtain, only a few sheep hunters are familiar with the area and knowledgeable about sheep population and harvest trends. In general harvest areas, many hunters hunt annually and become more attuned to wildlife population trends, hunter impacts, and needed management changes. Our barometer of satisfaction with TMA management is hunters with little or no experience in the area and with views based on limited perceptions. With little first hand knowledge there is little basis for the public to recommend changes to the hunt management. By interpreting the scarcity of complaints and recommendations as public acceptance, we may have perpetuated a management regime the public would not have supported had they had more experience in the TMA.

Our sheep population and harvest data indicated ram numbers and hunter behavior were changing in ways that might conflict with the intent of the TMA. There are management options that might enhance production of large horned rams in the TMA but those options would require regulatory changes. Prior to this survey, we did not know if hunters would desire changes in TMA hunt management strategies.

What does the public think about TMA management?

Overall, respondents overwhelmingly supported the current TMA objectives designed to enhance and maintain trophy sheep hunting and uncrowded hunting conditions. Most respondents believed very restrictive participation standards (the chance of drawing a TMA permit is <5%) should be continued in order to maintain these conditions. Most hunters believe hunting the TMA is a once-in-a-lifetime experience and quality of the hunt should not be compromised by increasing opportunity. This substantiated the past Alaska Board of Game decision not to adopt the proposal to increase hunting opportunity.

The largest respondent group, the Contents, is satisfied with current TMA hunt management. Based on hunter profiles and narrative answers from the questionnaire, this group includes the greatest variety of views on TMA management. The majority of this group view any full curl ram as a trophy, are not disappointed if they do not see a ≥ 40 inch ram and are more disappointed if they do not harvest a ram. By comparing answers to a series of questions, this group includes some hunters who are the most ardent trophy hunters.

The common ground between the contrasting harvest philosophies within the Contents group was maintaining hunting opportunity. Basically, a hunter who wants a TMA ram with exceptional horns requires 2 conditions, an opportunity to hunt and the availability of exceptional rams. Increased hunter participation and harvest combined with reduced trophy ram production due to poor lamb survival during the early 1990s have caused some decline in the number of large rams. However, the TMA still produces a relatively high number of rams with horns ≥ 40 inches when compared to most areas of Alaska. The most difficult aspect of hunting the TMA for these highly experienced hunters is obtaining permits, resulting in little support for further reducing opportunity. For the remainder of the Contents group, having the opportunity to hunt Dall sheep in pristine conditions and having a high probability of success are the primary attributes of the TMA. They believe those qualities are currently met under the present system and opportunity should not be reduced.

The Trophies have the strongest support for managing for trophy rams. They are willing to reduce opportunity to enhance trophy ram production. As a group, they are more discerning about what constitutes a trophy ram and more strongly support management based on horn length. Even considering how difficult it is to get a TMA permit they are willing to forego harvesting a ram if they do not see what they want.

The other 2 groups, Purists and Opportunities, represent a small number of the respondents. The wishes of the Opportunities group conflict with the intent of the TMA; thus these desires cannot be met without changing TMA management goals. Furthermore, their desires are currently met in the general Dall sheep hunts that occur in most Alaska sheep habitat excluding National Parks. The management direction preferred by the Purists, reducing the number of people who currently use the TMA to further protect its integrity, does fit the intent of the TMA. This group would side with the Trophies in supporting regulatory changes that would reduce opportunity but for a different reason.

MANAGEMENT IMPLICATIONS

Different views by different groups concerning trophy management direction in the TMA poses a dilemma. Do we manage to satisfy minority groups supporting hunter opportunity restrictions to increase production of large horned rams and/or reduce the chance of hunter crowding or do we follow the majority and maintain current regulations and hunter opportunity? Maintaining the current harvest management would satisfy the majority of the respondents, but for only 1 of the 4 user groups.

The key to hunter satisfaction in the TMA is preserving the opportunity to hunt trophy rams in uncrowded hunting conditions. There was disagreement on how to achieve those conditions among the 4 identified groups because of the range of trophy ram definitions, what is acceptable crowding, and what is adequate opportunity. However, based on rankings of possible management options, there seems to be some common ground between the Trophies, Contents, and Purists. The 1st or 2nd preferred option for all groups was to maintain the current number of permits but subdivide the TMA into smaller areas with permit drawings. Under this option, trophy ram production could be enhanced, uncrowded hunting conditions could be maintained and overall opportunity would be maintained. An additional permit allowing the recipient to hunt anywhere in the TMA would satisfy hunters wanting the greatest flexibility to hunt. From the manager's standpoint, hunt management could also be designed to better match sheep distribution and hunter access, thereby enhancing trophy ram production.

These results suggest changes should be made in TMA regulations. However, we suspect major changes in TMA's hunt structure will cause turmoil among hunters if the new regulations are believed to diminish their chances of being drawn or the new regulation reduces hunt quality or diminish their chances of being drawn. Again, because the TMA permit has become so hard to get, the arguments raised against any new management will be based on their perceptions of the past. The question to managers becomes: Will changes in management direction help to achieve management objectives?

Expected arguments against change would stem from the fact that current goals and objectives of the TMA are being met. Because most respondents would be satisfied by harvesting a full curl ram, changes to the TMA hunt structure to increase ram size could cause conflict. However changing the hunt structure by following the results of this questionnaire would be a benefit. Instead of meeting the desires of only one group (77% of the hunters) we might satisfy the desires of 3 groups (97% of the hunters).

Public opinion is important to wildlife management and should be part of the decision making process. However, in the case of drawing permit hunts, few hunters are knowledgeable about the area and the wildlife population. We believe lack of knowledge inhibits the public from recommending or possibly supporting regulatory changes until major changes in the hunted population or hunter use have occurred. In areas with this type of management, we believe questionnaires like this are invaluable for identifying who is using the area and what they desire. It is then the responsibility of the managing agency to use these results in combination with biological and harvest data to design the best management direction.

We recommend when other special hunt areas are established that goals, objectives, and any special terms are well defined at the onset. Some of the management dilemmas we are facing with the TMA could have been averted if terms like trophy ram and uncrowded hunting were better defined. By having better-defined goals and objectives the managing agency will have an easier time making timely changes based on population and hunter use data.

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MOUNTAIN GOAT INVENTORY IN THE ROBSON VALLEY, BRITISH COLUMBIA

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Abstract: A random sample unit survey using sightability correction was used to estimate mountain goat (*Oreamnos americanus*) population size along the Robson Valley in east-central British Columbia in August 1998. Twenty random sample units (12.4 ± 0.67 [SE] km^2 area) were surveyed in a 2,707-km^2 census zone above the 5,500-foot (1675 m) contour line. Standard helicopter survey techniques were employed to thoroughly search each unit (mean survey effort of 3.8 ± 0.21 min/km^2). Twelve radio-collared goats within the census zone provided sightability correction. We counted 127 mountain goats in the 20 units, covering 248 km^2 (9.2% of the census zone). The uncorrected population estimate for the census zone was 1,400 ± 260 goats (95% CI 900 to 1,900), and the mean density was 0.51 goats/km^2. Observers saw 8 of 12 radio-collared goats (67%), giving an adjusted population estimate for the census zone of 2,100 (95% CI 1,200 to 3,800), and an adjusted density of 0.77 goats/km^2. Accuracy and precision of future surveys could be increased by accurate stratification, sampling more units, using more marked (collared) goats, and ensuring that the marked segment of the population better reflects the composition of the census population.

Techniques to accurately estimate mountain goat (*Oreamnos americanus*) numbers in large remote areas are lacking. Practical sightability models or a reliable mark/resight or double sampling methodology have not been well-tested (Resources Inventory Committee 1997). Goats often occur in heterogeneous alpine and subalpine habitats, goat group size and habitat use are highly variable even within survey zones, and study area stratification is often difficult because prior knowledge of goat distribution is lacking. The heterogeneous nature of mountainous terrain and the frequency of forest use by the survey population likely affect sightability (Houston et al. 1986). Estimates of the proportion of goats seen using standard aerial survey techniques were about 68% in 2 studies (Cichowski et al. 1994, Gonzalez-Voyer et al. 2001), but may range as low as 30% (Hebert and Langin 1982, Smith 1984, Smith and Bovee 1984). Mark-resight estimations using radio-collars (46% sightability; Smith and Bovee 1984) and paint-marking (Cichowski et al. 1994) have been attempted on goats, however more testing is needed. The current British Columbia (B.C.) standard for goat inventory is a total count with accuracy confirmed by mark-resight (Resources Inventory Committee 1997).

The mountains surrounding the Robson Valley in east-central B.C. appear to contain a moderate to plentiful abundance of mountain goats, however, total count surveys have only been conducted on small areas within the region (Hebert and Smith 1986; B.C. Ministry of Environment, Lands and Parks (MELP), Prince George, unpubl. surveys). Although hunter harvest of goats in the area appears to be relatively light (averaging about 15 goats/year; MELP, Prince George, harvest statistics), concerns with the impacts of expanding forestry development prompted initiation of a radio-collaring study in 1997 that is examining low elevation forest use (Poole 1998, Poole and Heard in 1998). Our objectives were to estimate mountain goat numbers within the region and to test a new technique (random sample unit survey using sightability correction provided by radio-collared goats) to derive this estimate.

STUDY AREA

The Robson Valley mountain goat study area flanks the Rocky Mountain Trench, which separates the Rocky Mountains to the east and the Cariboo Mountains to the west. The area is made up of 4 of biogeoclimatic zones: Sub-Boreal Spruce (SBS) and Interior Cedar-Hemlock (ICH) zones in the Trench, through the Englemann Spruce-Subalpine Fir (ESSF) zone to the Alpine Tundra (AT) zone with increasing altitude. Treeline is between 1900-2150 m (6,250-7,050 ft). Climate varies with elevation. Mean July and January temperatures for Valemount, located in the Trench at 800 m roughly in the centre of the study area, are 15.8 and –11.0°C, respectively, with an average of 503 mm of precipitation annually (Environment Canada climate normals, unpublished data). In the Trench and valley edges hybrid white-Engelmann spruce (*Picea glauca* x *engelmannii*), subalpine fir (*Abies lasiocarpa*), western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*) are the dominant trees, with extensive stands of lodgepole pine (*Pinus contorta*) due to frequent fire disturbances (MacKinnon et al. 1992). Higher up the mountainsides spruce, subalpine fir and lodgepole pine dominate, with scattered stands of whitebark pine (*Pinus albicaulis*) at the highest elevations. Douglas-fir (*Pseudosuga menziesii*) trees are found throughout the area. In the AT zone conifers are present only in stunted krummholz forms.

The study area was selected to include the front ranges off the Robson Valley, where most hunting effort was concentrated, and all mountain blocks (relatively discrete areas of alpine surrounded by lower elevation forested habitat) containing radio-collared goats (Fig. 1). Mountainous habitat to the southwest of McBride was excluded because of a wildfire and large amount of helicopter activity at the time of the inventory. We used lakes, rivers, large glaciers and height of land to bound the 6,400 km^2 study area. Within the study area we selected a census zone above the 5,500-foot (1,675 m) contour line because, A) this contour bounded the lower limit of the summer distribution of radio-collared goats (Poole 1998), B) there were few cliffs below this level, C) the 5,500-foot contour line was readily identified on topographical maps, and D) the altimeter of our helicopter was in feet. The census zone covered 2,707 km^2, and included portions of B.C. MELP wildlife management units (WMU) 7-2, 7-3, and 7-4.

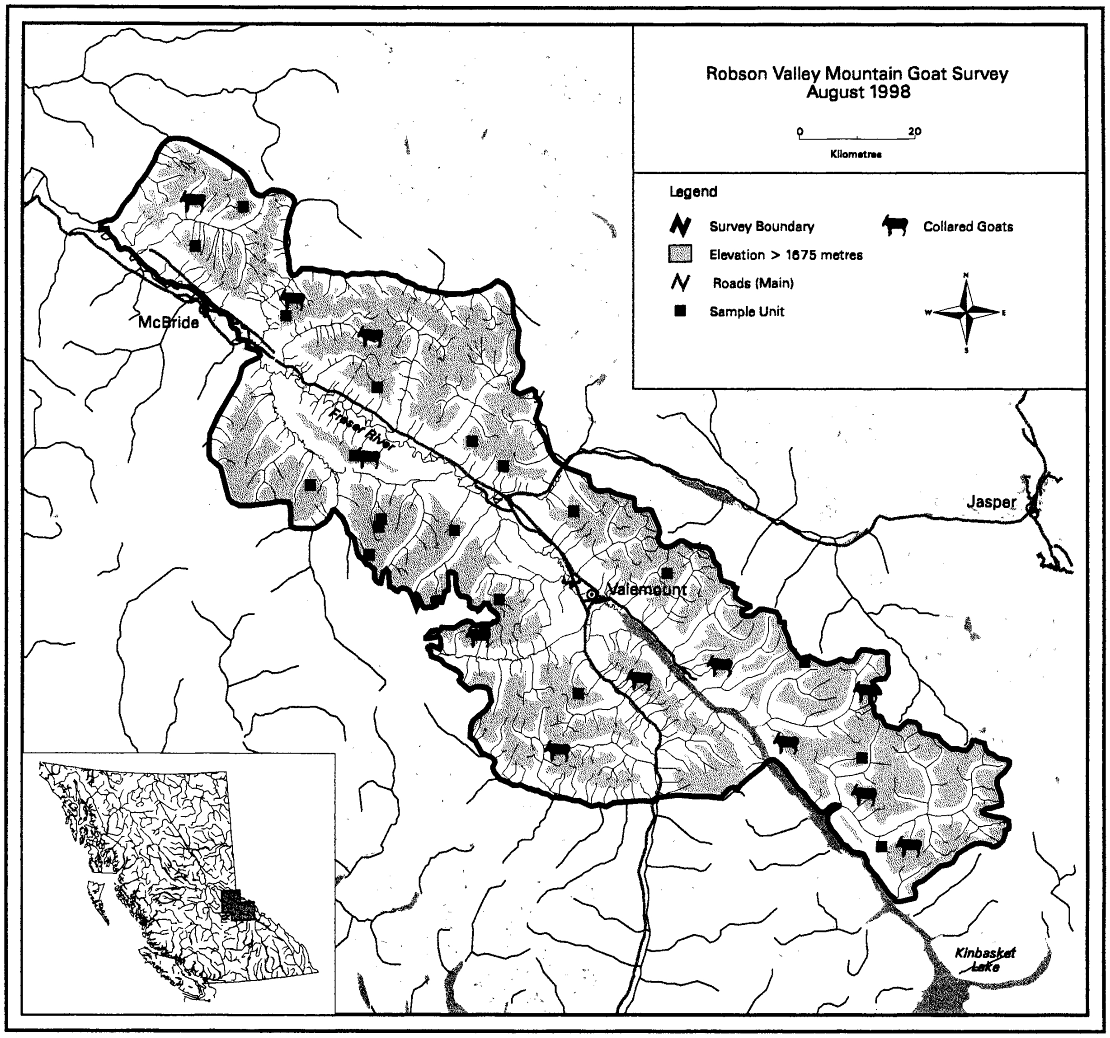

Fig. 1. Robson Valley mountain goat survey showing study area (heavy line), census zone (gray shading), sample units (boxes) and radio-collared goats (goat symbol), 17-21 August 1998.

METHODS

Sampling strategy

We did not stratify the census zone because we had no reliable prior knowledge of mountain goat distribution. We selected sample units using a random numbers table to generate points on a survey map. All points located within the study area were used; points located below the 5,500-foot level were moved up-slope into the census zone. We used these points as the starting point for the survey of each sample unit. This method is not strictly appropriate (Caughley and Sinclair 1994), but worked well in this study because sampling intensity was low. We did not randomly select from among predefined sample units because of the time and cost required to conduct this for the entire census zone.

We conducted the census between 17 and 21 August 1998. We used a Bell 206B Jet Ranger helicopter with pilot, navigator, and 2 observers. The pilot and navigator remained the same throughout the census but observers changed. All occupants participated in locating mountain goats. Starting at the lowest elevation, we flew 100-150 m contour lines at 60-90 km/hr, 50-75 m out from the hillsides. Sample units were surveyed for 35-55 minutes, so that discrete units were covered, generally entire mountain blocks or valleys. We determined boundaries of sample units by using obvious features on the topographic maps, generally height of land between drainages. Sample unit shape varied with terrain, and we determined the size of individual units using a GIS. Sample units did not overlap. We mapped flight lines, survey coverage and location of goats on 1:50,000 topographical maps and recorded the elevation (to the nearest 100 feet) of the goat group from the helicopters altimeter. We classified goats only into kids and adults (yearlings and older) based on body size (B. L. Smith 1988) to reduce survey time, to minimize harassment (Côté 1996), and because researchers familiar with classification from aircraft agree more detailed age and sex classification is not reliable (Houston et al. 1986, Stevens and Houston 1989, Gonzalez-Voyer et al. 2001, S. Coté, Université de Sherbrooke, personal communication).

Sightability correction

On 16 August all 12 radio-collared mountain goats (10 nannies and 2 billies) in the census zone were located by the navigator using a fixed-wing aircraft. During the subsequent 5-day census an attempt was made to locate each radio-collared goat. The navigator was able to monitor goat location using telemetry gear attached to the helicopter and audible only to the navigator. We conducted 12 sightability tests to estimate the proportion of radio-collared goats that observers see under survey conditions. Sightability test plots were centred near the last location of a radio-collared goat, and survey of these blocks was conducted as if they were a standard sample unit. We believe there was no bias in the chances of seeing a collared goat compared to any unmarked goat because we started each sightability test sample unit survey at a defined (topographic) edge of the unit (away from any marked goat), and we attempted to make sample unit coverage even in all surveying. In most cases the observers were unaware that they were being tested for sightability (i.e., that there was definitely a goat nearby). Three radio-collared goats happened to be in random sample units. We did not use mountain goat count data from the sightability test plots for density or composition calculations.

To correct for the sightability bias, we estimated the fraction of radio-collared goats seen by observers in test plots, $p_1=m_1/n_1$; where m_1 is the number of radio-collared goats that were seen by the observers, and n_1 is the number of radio-collared goats in the test plots. The variance of p_1 was based on the binomial distribution, var = pq/n because each radio-collared goat was an independent sample (Snedecor and Cochran 1967).

Data analysis

We calculated the observable population estimate and its variance based on Jolly (1969) for unequal sized sample units where the maximum number of sample units in the census zone was estimated by dividing the average sample unit size into the area of the census zone. The census zone population estimate is equal to the observable population estimate divided by p_1 (the fraction of radio-collared goats seen during the sightability tests). Because the population estimates were not normally distributed but right skewed (Caughley and Sinclair 1994), we calculated the 90% confidence intervals for all estimates using a Monte Carlo simulation model with 5,000 trials.

RESULTS

We counted 127 mountain goats in 54 groups in 20 sample units, covering 248 km^2 (9.2% of the census zone). Only 1 sample unit had no goats present and the maximum unit count was 17 animals (Fig. 2). Group size ranged from 1 to 10 with a mean (± SE) group size of 2.4 (± 0.31). "Typical" group size, an animal-centred measure of the group size within which the average animal finds itself (Jarman 1974, Heard 1992), was 4.5 (± 0.29). Even though 74% of groups consisted of 1 or 2 animals, 40% of the animals were in groups ≥ the typical group size (Fig. 3). Mean time on each sample unit was 44.7 ± 1.63 minutes and mean area covered for each sample unit was 12.4 ± 0.67 km^2, giving a mean survey effort of 3.8 ± 0.21 min/km^2 (n = 20). The naïve (uncorrected) population estimate for the census zone was 1,400 ± 260 goats (95% CI 900 to 1,900), and the mean density was 0.51 goats/km^2. Extrapolated to the entire study area, the mean density was 0.22 goats/km^2.

Observers saw 8 of 12 radio-collared goats (67%), giving an adjusted population estimate for the census zone of 2,100 (95% CI 1,200 to 3,800), and an adjusted density of 0.77 goats/km^2. Mean group size of collared goats was 3.3 (± 0.84), and ranged from 1 to 9 goats (n = 11; 1 collared goat was not observed after the sightability trial, despite intensive effort). Fifty-five percent of the collared groups consisted of 1 or 2 goats. Mean group size did not differ between censused goats and collared goats (t = 2.0, P = 0.24).

Kids comprised 25% (± 3.4%) of censused goats. The elevations of censused goats and radio-collared goats were almost identical (Table 1). Most censused goats were found in the 7,000-7,400 foot band (Fig. 3). Groups with kids were found at the same elevations as groups without kids (Table 1; t = 1.1, P = 0.28). Mean number of adults in groups with kids (2.8 ± 0.43) was greater than adult only groups (1.1 ± 0.06; t = 3.8, P = 0.0012). Similarly, typical group size (kids removed) was also greater for groups with kids compared with groups without kids (4.1 ± 0.29 vs. 1.3 ± 0.07; t = 9.5, P = 0.0001).

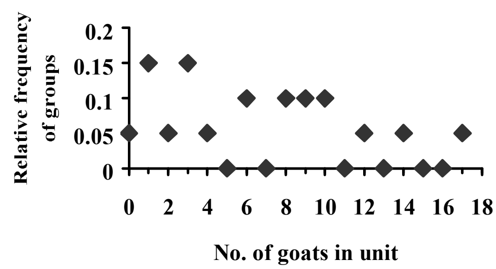

Fig. 2. Relative frequency distribution of number of mountain goats in sample units (n = 20), in the Robson Valley, 17-21 August 1998.

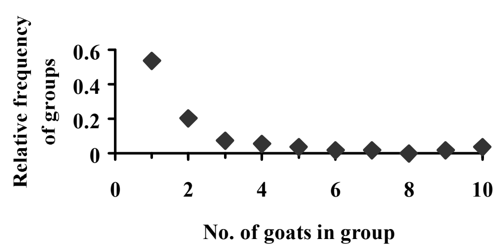

Fig. 3. Relative frequency distribution of mountain goat groups (n = 54), in the Robson Valley, 17-21 August 1998.

Table 1. Elevation of mountain goat groups observed during the census and of radio-collared goats used for sightability correction, Robson Valley, 17-21 August 1998. Three of the radio-collared goats were counted during the census, and are shown in both collared and censused goat groups.

	n	Mean (SE) elevation (ft)	Median elevation (ft)	Min. elevation (ft)	Max. elevation (ft)
Collared goats	12	6,960 (183)	7,000	5,900	7,800
Censused goats	54	6,970 (73)	7,000	5,500	8,100
Non-kid groups	34	6,910 (92)	7,000	5,500	8,100
Kid groups	20	7,080 (120)	7,100	6,000	7,900

DISCUSSION

A number of assumptions must be met to validate mark-resight estimates (Caughley 1977), most of which were likely met in the current study (i.e., there was geographic and demographic closure, no loss of collars, no overlooked collars [marks], goats were not counted more than once, and aerial samples were independent). We observed minimal movement of collared goats from immediately before the survey to during the survey, and the survey was conducted over a short period of time, thus it is unlikely that there was more than a minute amount of movement of goats into or out of the census zone or among sample units. However, the assumption of equal catchability (the collared goats were representative of the "true" population) may have been partially violated. Billies comprised only 2 of the 12 collared goats. Since group size has been suggested as a significant variable explaining visibility bias to detect mountain goats (Strickland et al. 1994) and other ungulates (Samuel et al. 1987), group size of billies is likely smaller than nanny-kid groups during summer (Wigal and Coggins 1982), and billies likely make up roughly one third of the true population (K. G. Smith, personal communication), our observed sightability may have been biased high. Support for this conclusion is given by observers sighting only 1 of the 4 radio-collared goats occurring as single animals, and all of the 7 collared goats in groups (>1 goat). More collars would have increased the precision of the population estimate.

Noteworthy is the fact that the proportion of marked goats observed during our study (67%) is very similar to proportions derived independently in other interior mountain goat populations using slightly different techniques (68%; Cichowski et al. 1994, Gonzalez-Voyer et al. 2001). The sightability of goats in coastal populations appears to be considerably lower (30-46%; Hebert and Langin 1982, Smith 1984, Smith and Bovee 1984). A number of factors contribute to goat sightability, but 65-70% sightability may serve as a standard for interior populations under "normal" survey conditions.

Population estimates based on mark-resight estimators are expensive to conduct because a reasonable sample of collared animals is required. Using a logistic regression estimator, correction factors are applied to each group observed during surveys (Anderson and Lindzey 1996). While a logistic regression-based sightability model may provide more practical and cost-effective population estimates, we suggest that it would be difficult to develop a mountain goat sightability model based on vegetation cover (as in Samuel et al. 1987, Anderson and

Lindzey 1996, Anderson et al. 1998) and terrain/topography (cliff size, shape and morphology). The study area is a heterogeneous mix of alpine meadows, shrubs, krummholtz, upper elevation forests, scree slopes, and varying-sized cliffs with varying degrees of shrubs and/or trees intermixed. Confounding variability in group size and environmental and behavioral factors, including sexual differences, would add to model complexity. A significant number of collared mountain goats would be required to obtain such visibility curves, and the applicability of such a model to other mountainous regions in B.C. would require verification.

Stratified, double sampling involving fixed-winged (Super Cub) surveys and logistic regression and Jackknifing procedures are currently used to estimate Dall's sheep (*Ovis dalli*) and mountain goat population size in Alaska (McDonald et al. 1990, Loranger and Spraker 1994). However, this technique will accurately correct visibility bias only when all goats seen during the initial (standard) survey are seen during the intensive resurvey, and when all goats present in the sample unit are seen during the intensive survey (Poole et al. 1998); neither assumption is generally met (Loranger and Spraker 1994, Strickland et al. 1994).

A stratified random survey design using fixed-wing reconnaissance flights has been used previously to survey mountain goats (Houston et al. 1986, van Drimmelen 1986). Houston et al. (1986) used previous knowledge of goat distribution to delineate 4 strata in the Olympic Mountains, Washington, but still had highly variable counts in their medium density stratum. In the Telkwa Mountains of west-central B.C., stratification was based on the length of steep cliff habitat, forage availability and vegetative community (van Drimmelen 1986). Accurate stratification enabled time savings of reduced effort in low strata, however high (57%) coverage of the 640 km^2 area was required to obtain a confidence interval of <20% of the estimate (90% confidence level). Even in hindsight, we saw no way to accurately stratify our study area, although goat density appeared to be slightly higher in the quarter of the census zone north and east of Highway 16.

The range in elevation covered by the collared goats was similar to that found in the census population, suggesting that our census zone covered a majority of the goats in the study area. Some cliffs are found below 5,500 feet elevation and have been used by the study goats, but generally not during summer (Poole 1998).

Uncorrected goat densities (0.51 goats/km^2 for the census zone, 0.22/km^2 for the entire study area) obtained during this study were generally higher than uncorrected densities (mean 0.15 goats/ km^2; range 0.08-0.31 goats/km^2) obtained from helicopter surveys (primarily conducted in 1982 and 1983) in 6,280 to 1,170 km^2-study areas in interior B.C. (Hebert and Woods 1984). Using stratified random sampling, van Drimmelen (1986) estimated 0.40 goats/km^2 in 640 km^2 of alpine and sub-alpine in the Telkwa Mountains in northwest B.C. Using a mark-resight method, Cichowski et al. (1994) estimated 0.87 goats/km^2 in a 324-km^2 area in the Babine Mountains of northwest B.C. We calculated an uncorrected density of 0.34 goats/km^2 from data reported from a total count survey conducted in a 6,400 km^2 area in the Hazelton and Coast mountains of western B.C. (Demarchi et al. 1997), approximately 50% higher than our uncorrected study area density. Comparisons of goat densities among studies must be conducted cautiously because of differences in study area size and definition, study design, survey timing and intensity, and other factors.

The proportion of kids we observed (25%) was higher than the percent kids observed during summer/early fall surveys in the Babine Mountains (17-18%; Cichowski et al. 1994), the Hazelton and Coast mountains (19%; Demarchi et al. 1997), and interior B.C. (15-23%; McCrory 1979, and 21%; Hebert and Woods 1984). However, direct comparisons may not be valid because kid estimates vary with survey techniques and time of year (Festa-Bianchet et al. 1994).

The number of goats shot in WMUs 7-2, 7-3 and 7-4 has remained relatively constant over the past 10 years, averaging 14.8 (± 1.41) goats annually, with no linear trend ($r^2 = 0.04$, $P = 0.6$). The proportion of billies in the kill averaged 59% (± 4.9%). The kill rate of 0.7%/yr (or 1.1%/yr using the lower 95% CI population estimate of 1,200 goats), is likely below the maximum sustainable yield for most populations (Houston and Stevens 1988, K. G. Smith 1988). Range-wide population and hunter kill estimates cannot be used to manage specific mountain blocks because of variable hunter effort and access across zones.

MANAGEMENT RECOMMENDATIONS

We suggest that a random sample unit survey has the potential to be used broadly for surveying mountain goats, especially over large areas where complete coverage is impractical. A number of changes would increase the accuracy and precision of future surveys:

1. Accurate stratification of sampling units into areas of similar density and the appropriate allocation of effort among strata (Caughley and Sinclair 1994).
2. Increase sampling intensity and provide a greater number of marked (collared) goats. Both the number of sample units and the number of goats marked would have to be tripled to obtain a coefficient of variation of about 0.1, an acceptable result for wildlife surveys (Sinclair 1972).
3. Ensure that the marked segment of the population reflects the composition of the census population.
4. Sample units should be predefined, and then those to be flown selected randomly (Caughley and Sinclair 1994).

Although it would be expensive and logistically difficult to develop, construction of a logistic regression sightability model may ultimately be the most practical and cost-effective approach for mountain goats inventories in B.C. (I. Hatter, B.C. MELP, Victoria, personal communication). However, sufficient numbers of trials with marked goats are required to run the sightability trials required to develop and quantify such a model. Data from moose (*Alces alces*) modeling suggest that at least 80, preferably >100 trials are required to produce a goat sightability model with reasonable variance and broad applicability (Anderson and Lindzey 1996, Anderson et al. 1998, MacHutchon 1998).

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POPULATION DYNAMICS OF BIGHORN SHEEP IN HELLS CANYON

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Abstract: Rocky Mountain bighorn sheep were extirpated from the Hells Canyon area of Oregon, Idaho, and Washington by 1945. Since 1971, 15 bighorn herds have been established through relocation of 415 sheep from 10 source populations. Reintroduced populations have exhibited various growth patterns, including high rates of growth for several years followed by reduced growth, and all-age disease epizootics. We examine historic and recent survey and monitoring data, describe patterns of population growth and adult and lamb survival, and evaluate hypotheses about the effects of population density, weather, distance to domestic sheep, source population, and other factors on Hells Canyon bighorn population dynamics.

DYNAMICS OF HUNTED AND UNHUNTED MOUNTAIN GOAT POPULATIONS

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Abstract: Native populations of mountain goats (*Oreamnos americanus*) are sensitive to harvest. To assess the potential effects of limited hunting on population dynamics, we analysed long-term data obtained from annual aerial counts of twelve mountain goat herds in Alberta from 1973 to 1999. Eight herds were hunted until 1987, and 4 were not hunted. Mountain goat numbers declined in most herds between 1980 and 1983, despite a decrease in the number of permits issued. Hunting was closed in 1987. We found that temporal changes in population size varied among herds over the same period, suggesting that herd-specific factors were responsible for these changes. Only 3 of 8 herds showed a marked increase after hunting was closed. The unhunted herds also showed substantial among-herd differences in population trends, suggesting that the impact of harvest varies among populations and that goat management must be herd-specific. Juvenile/adult goat ratios based on aerial surveys were not clearly associated with harvest levels, and were only slightly affected by weather conditions, but these ratios are a poor estimator of recruitment. Our results suggest that factors other than harvest contributed to the population decline. Future harvests should target adult males, but in an intensively studied population adult sex ratio was heavily biased in favor of females. A herd of 100 goats may only sustain the harvest of 1-2 adult billies a year.

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DALL'S SHEEP (*OVIS DALLI DALLI)* SEXUAL SEGREGATION: ENVIRONMENTAL FACTORS AND SPATIAL IMPLICATIONS

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Abstract: Sexual segregation is a characteristic of polygynous ungulates, and it has been documented among many species in temperate-cold climates. However, reasons for this phenomenon and its potential use in conservation and management remain poorly understood.

I carried out my study during summer at Hoge Pass, Kluane National Park, Yukon. Objectives were to observe and determine the location of sheep groups, relating habitat and group characteristics. I tested two hypotheses reviewed in Main *et al*. (1996):

1) Dall's sheep socially segregate, because rams are trying to optimise their fitness, foraging in the best patches of vegetation, which also are areas with higher predation risk. Ewes of the same population are selecting habitats for raising their offspring (low predation risk), using cliffs or talus (security terrain) where food availability may be lower.
2) The proportions of security terrain, vegetation distribution, quality and availability determine the spatial segregation of Dall's sheep at Hoge Pass. Males distribute themselves in habitat with higher quality and availability of vegetation, and further from security cover; while females were expected in habitats with lower quality and availability of vegetation, but closer to security cover.

Collected data were used to generate a regression model of sexual segregation, to provide data for management guidelines, and to explain potential causes of sexual segregation in ungulates.

Biennial Symposium Northern Wild Sheep and Goat Council 12:128-137.

THE FOUNDATION FOR NORTH AMERICAN WILD SHEEP – A SHEEP BIOLOGIST'S VIEW FROM THE INSIDE

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Abstract: Sheep managers, researchers, and wildlife management agency administrators throughout North America recognize the Foundation for North American Wild Sheep (FNAWS) as the major non-governmental funding source for sheep conservation in North America. Many sheep managers are members of the Foundation, and work closely with the Foundation's staff and Board in coordinating fundraising for projects. Since its inception 25 years ago, the Foundation has raised and spent almost $25 million in pursuit of its directive, "to put more sheep on the mountain." The results have been notable, particularly a reported doubling of bighorn numbers over the last 25 years. Still, few wild sheep managers, and even fewer agency administrators understand how the Foundation actually works. FNAWS is unique among non-government organizations (NGOs) in that it shares a certain tension with management agencies that is more clearly defined than that of the management establishment with other NGOs. Over time, it has become clear to FNAWS that this agonistic relationship is the result of general abdication of management responsibility for mountain sheep, and means FNAWS is definably less likely to "trust the agency" than are other NGOs. The root of this difference lies in the Foundation's growing perception that management agencies don't fail in sheep management for lack of money as much as for lack of commitment to sheep as a priority. As a result, FNAWS is more likely to be involved in management actions than other NGOs. Changes in funding mechanisms over the years, from complete dependence on donated hunts, to "Governor's permit" auctions, and the "New Beginnings" endowment have begun to change the relationship between FNAWS and managing agencies. The change seems certain to continue. These changes will be discussed to stimulate thinking and make managers more fully aware of the new climate in which FNAWS may be expected to operate.

Disclaimer: This account is not to be understood as a review of the Foundation for North American Wild Sheep (FNAWS) history. It represents my observations on the status of the relationship between the Foundation and the profession…from a former professional sheep manager to other wildlife professionals. A detailed history of FNAWS (Schultz et al. 1999) is available from the Foundation. [WEH]

My journey with the Foundation for North American Wild Sheep began with perception and has continually approached reality over the 25 years during which I have been associated with FNAWS. I first heard of FNAWS shortly after it had been formed. Given the tenor of those times, I guessed it was yet another "trophy-crazed bunch of sheep hunters." Still, even as a rookie sheep researcher and manager, I'd developed a deep respect and admiration for sheep hunters because of their dedication to sheep and their interest in, and willingness to support, doing the right things for sheep. In short, I'd come to perceive sheep hunters as important partners. Hence, I embraced FNAWS as a potentially viable source of support for progress in sheep management throughout North America even though I had no idea how they'd actually "put more sheep on the mountain." After a quarter of a century of association with FNAWS, I'm pleased to report FNAWS is far more than a "trophy-crazed bunch of sheep hunters." FNAWS is for real, and appears to be here to stay.

HOW THE FOUNDATION WORKED: THE EARLY YEARS

The original approach taken by the Foundation's founders was to incorporate as a non-profit organization. Next, the Foundation persuaded guides and outfitters to donate guide services for hunting (generically referred to as "hunts") to the non-profit organization. These hunts were then auctioned to the highest bidder at the Foundation's national convention, thus creating tax benefits (resulting from contributions to the non-profit Foundation) for the buyers. The income from these hunts, minus minimal administrative costs, was then made available as grants to fund sheep management and research projects to "put more sheep on the mountain." Over time, the success of the Foundation has been notable.

EARLY RESULTS

According to Duncan Gilchrist's tabulations (from Trefethen 1974), when the Foundation was organized, the best estimate of bighorn sheep numbers in North America was about 34,000 sheep. Twenty-five years later, the Foundation had been instrumental in raising (and spending) $25 million, and the estimated number of bighorns (Gilchrist's tabulation from the 2nd North American Wild Sheep Conference of 2000) had increased to 74,000. It is logical to suppose that some of this increase resulted from increased counting effort or efficiency. Nevertheless, there has been an apparent increase of approximately 40,000 sheep over 25 years. This 'doubling' of bighorn numbers has been coincidental with expenditure of 25 million FNAWS-generated dollars.

Here it should be emphasized that not all of this money has gone to sheep restoration and management through FNAWS grants. Some "hunt auction proceeds" have been returned to hunt donors to cover their expenses, and some have gone to run the Foundation. The remainder has been disbursed through the FNAWS Grant-In-Aid program. When "Governor's permits" developed (see Erickson 1988 for a short history), huge sums of money were generated which reverted directly to state and provincial management agencies with "gentlemen's agreements" that these dollars would supplement donor state or province agency budgets for sheep management and restoration. Some states and provinces have abided by these agreements more than others have.

Simple calculations based on the amount of FNAWS-generated money, elapsed time, and the reported increase in bighorn numbers yield the following statistics: The increase in bighorn sheep (40,000 over 25 years) averaged approximately 1,700 sheep per year. Also, dividing 40,000 sheep into $25 million indicates an average cost of $625 per sheep. Total monetary costs to produce the reported increase in bighorn numbers were probably somewhat higher because state and provincial management agencies spent some non-FNAWS-generated dollars on sheep along the way. However, the few documented agency sheep budget increases over the last 25 years (see Pybus and Wishart (eds): Status Reports Ninth North. Wild Sheep and Goat Counc. Proceedings, 1994), seem to have followed sheep population increases, they certainly did not pre-date (and hence cannot be considered a cause of) the increases in bighorn sheep numbers. These circumstances raise the question, "Would bighorn sheep numbers have increased without FNAWS?

POSSIBLE CAUSES OF BIGHORN POPULATION INCREASES

Biologists are, of course, interested in identifying whether the correlation between FNAWS fundraising, the resultant increases in agency expenditures, and increases in bighorn populations were causally linked. I suggest they were; here's why:

Obviously, bighorn sheep populations will increase whenever recruitment exceeds mortality. In this case, there is no reason to postulate bighorn populations were already increasing when FNAWS was formed. Review of the Transactions of the Desert Bighorn Council and Northern Wild Sheep and Goat Council Proceedings prior to 1974 indicates few, if any, thriving bighorn populations. The common thread linking papers presented at these meetings was struggling or declining populations threatened by grazing competition, disease problems, and habitat loss.

For bighorn populations to "turn around" in 1974 would have required abrupt decreases in environmental resistance to bighorn population growth coincidental with FNAWS formation. Viable alternate hypotheses would require supporting evidence documenting continent-wide decreases in overall environmental resistance to bighorn population growth. To consider this possibility, overall environmental resistance to bighorn population growth may be divided into its identifiable components.

Overall environmental resistance may be thought of as the sum of human harvests, non-human predation, negative weather effects, and decreases in habitat quality. Three of these components appear more likely to inhibit bighorn population growth at present than in the past. Mortality resulting from increases in human harvests, weather-related increases in environmental resistance, and non-human predation have *apparently increased* during the last quarter century.

Human harvests have increased commensurate with increases in overall bighorn population size (see Thomas and Thomas 2000 status reports). Also, harvest by humans is still traditionally focused on mature rams. This mature ram harvest has minimal effects on productivity and survival. Harvests of ewes designed to limit bighorn population growth have been generally insignificant continent-wide. Hence, it is highly unlikely that decreases in human harvests have contributed to the continent's doubling of bighorn sheep numbers.

Review of the published literature suggests weather has been, if anything, generally less favorable to bighorn population growth over the last 15 years. Activity of *El Nino* and *La Nina* appears to have produced less stable and relatively harsher winters in northern habitats accompanied by drought in southern habitats. Although changes in weather cycles appear to have taken place over the last 25 years, I know of no data suggesting that weather has become *more* favorable to bighorn sheep over that period of time. Also, for what it's worth, climate scholars and advocates of global warming theory have yet to postulate a benefit from this phenomenon.

Mortality resulting from non-human predators has also apparently increased during the last 25 years. Restoration of mountain lion populations, reintroduction of wolves, increased populations of eagles, expanding coyote populations, and protection of predators as a human societal choice have predictably resulted in greater predator abundance. Increasing mortality from non-human predators is being reported by an increasing number of authors, and may be the most compelling management issue in the shorter-term future.

In spite of the fact that actions of these components of overall environmental resistance should have produced lower, not higher, bighorn numbers, reported bighorn numbers have doubled. By elimination, this leaves improvements in habitat quality or quantity as the most robust hypothesis rationalizing the reported increase in bighorn numbers. The cause of this increase in habitat quantity/quality has been re-introduction of bighorn sheep to former ranges. Hence, it may be logically argued that active management, primarily through transplantation to effect bighorn re-introductions, has been the primary cause of increased bighorn numbers throughout North America during the last 25 years. This active management has created a tension between FNAWS and state/provincial management agencies, which sets FNAWS apart from typical non-governmental organizations (NGOs).

THE UNIQUE FNAWS ORGANIZATIONAL CULTURE (OR CHARACTER)

The organizational culture of FNAWS is unique among NGOs. FNAWS is more likely to be unabashedly pro-hunting than most NGOs. I suggest this is primarily because FNAWS revenue is hunter-driven by design. This specific pro-hunting stance, as well as a specific organizational culture built around "more and better traditional sheep hunting," makes FNAWS more proactive with respect to management and political issues than typical NGOs.

At the basis of the FNAWS organizational culture is the unarguably, fact-based perception that state and provincial management agencies have historically made sheep restoration and management a low priority. As a result, FNAWS has developed a sort of "noble crusader" mentality, which influences FNAWS/agency interactions. I suggest the basic reason sheep management was never afforded a high priority was that sheep populations were virtually nonexistent when traditional wildlife management was evolving and its financial base was being developed. I consider the linkage between these two aspects of management critical to understanding the unique character of FNAWS compared with other NGOs.

Wildlife management requires money. In the United States, availability of money is linked to sales of hunting licenses. Because there were basically no sheep to hunt when the ethos and funding mechanism of wildlife management developed (75 to 50 years ago), early managers reasoned there was "no profit" to states or provinces from sheep management. The investment in restoration before any profit could be realized was considered (if at all) a "long shot" or poor risk. Consequently, revenue-producing species such as deer, elk, moose, caribou, bears, and small game dominated management's thinking, and were established as high priority programs. The result was that sheep were generally ignored. As management philosophy broadened in modern times, trendy programs like non-game management simply leapfrogged sheep management on the priority scale. Sheep management funding continued at the traditional level. FNAWS has noticed the priority of sheep management appears to be more tightly linked to management tradition than available funding.

When FNAWS, an organization zealous for sheep, emerged with the willingness and money to "put sheep on the mountain," it was shocked by the prevailing management attitude. Rather than adopt the existing management philosophy, FNAWS aggressively undertook sheep management and restoration, often in spite of resistance by, or with the grudging consent of, upper level state and provincial wildlife officials. This administrative resistance was also noted by the Foundation. The administrative attitude was in marked contrast to the enthusiasm of field biologists and managers who were already deeply committed to sheep restoration and management. Within this fairly tense organizational climate, FNAWS began to provide funding for sheep restoration and management projects in a less-than-systematic fashion. The term "shotgunning" has been a reasonably accurate descriptor articulated by some biologists. FNAWS also funded a great deal of what many call research, but because of my bias that meaningful research is a part of management, I have not separated the 2 here.

The low average cost per sheep ($625) produced over the last 25 years suggests that the agencies based their traditional low prioritization of sheep programs on flawed thinking. While sheep management might not, as yet, put a management agency deeply in the black, other programs, which offer even lower prospects for generating revenue, have received higher priority than sheep. Still, many sheep programs have reached the point where they, with FNAWS-generated funding, typically pay their own way in terms of operational budgets.

Nevertheless, the historic low agency priority for sheep management based on questionable justifications has created and maintained a tension between FNAWS and state and provincial management agencies which is atypical for NGOs. Typically, NGOs have very high confidence in the decisions of state and provincial management agencies, and are satisfied to simply provide supplemental funding for use according to priorities established by the management agency. In contrast to this norm, FNAWS has developed a tradition of questioning agency motives and priorities, as well as a certain suspicion that agencies would prefer to use FNAWS-generated money for traditional priorities. This suspicion is not without foundation, and agency leaders would do well to re-examine their traditional priorities.

The unique FNAWS character also arises from differences in approach compared to those of other NGOs, which have defined the "agency comfort level" for relationships with non-governmental funding sources. The more successful NGOs are heavily habitat-oriented. That is, typical NGOs operate on the basic assumption that if existing habitat can be preserved or enhanced, all will be well with their species of special interest. I can identify only 2 NGOs that focus on transplant or re-introduction of favored species to new habitats, FNAWS and the National Wild Turkey Foundation. State management agencies have been greatly more inclined to re-introduce or establish transplanted populations of turkeys because the revenue-generating potential is higher, realized in a shorter time, and turkeys are more easily managed. For this reason, turkeys thrive in areas where they are introduced fauna, while significant amounts of historic bighorn sheep habitat have yet to see a sheep in modern times.

Compounding the adaptive agency preference for revenue-producing species is the complexity of wild sheep management. While North American wild sheep do have hooves on the ends of their feet and are by definition ungulates, their suite of adaptations to climax habitats appears to be basically different from those of seral-adapted species (e.g., deer) which drive classic ungulate management (Heimer 1999*a*). In addition to a differing set of adaptations (particularly among thinhorns), wild sheep have an associated liability resulting from failure to adapt in the short-term.

Susceptibility to diseases endemic to domestic sheep must be considered in wild sheep management. Successful bighorn restoration and profitable management of bighorn (and thinhorn) populations require management of this disease liability. At present the only promising technique for maintaining viable wild mountain sheep populations is exclusion of domestic sheep from their habitats. This means a bighorn manager must face the down and dirty work associated with negotiating, establishing, and maintaining separation of bighorns from domestic sheep. The most successful approach to reclaiming bighorn habitats from domestic sheep involves negotiating and funding retirement of domestic sheep grazing allotments on bighorn ranges. This is hard administrative work, and not a particularly preferred activity for field biologists or administrators in states with traditions of domestic sheep ranching. Nevertheless, cooperation between federal agencies, most notably the US Forest Service and Bureau of Land Management, FNAWS, state wildlife management agencies, and progressive ranchers has produced significant progress in this area. This progress, of course, results in increased availability of habitat where bighorn sheep can be reintroduced with a reasonable probability of eventually producing revenue for the states involved. These efforts have contributed to the "habitat bonanza" responsible for the doubling of bighorn numbers over the last 25 years. This has been a very expensive process in terms of both effort and money.

RECENT FNAWS FAILURES: PERCEPTION AND REALITY

In recent years FNAWS has had virtually no money to allocate through the traditional Grant-In-Aid mechanism. Many biologists have been puzzled by this situation, wondering how FNAWS can report apparently huge convention "profits," but still not have money available for Grants-In-Aid. Basically, the reason is: *FNAWS really doesn't get to administer most of the money it raises.*

Prior to the advent of "Governor's permits," FNAWS money for support of sheep management (Grant-In-Aid money) was generated at the annual FNAWS convention through the sale of donated hunts. This is still the case, but that's not where the "big money" FNAWS reports from a successful convention is generated. The big money comes from auction of Governor's permits.

Many state and provincial Governor's permits bring tremendous prices at auction, and FNAWS rightfully enjoys taking credit for maximizing the funds raised through auction of these permits. When FNAWS includes these permit sales in the "annual dollars raised" figure reported from a successful convention, the number is high! However, as a condition of Governor's permit donations, typically 90% of this money goes directly back to the states or provinces that donated the permits to FNAWS for auction. The FNAWS function here is not administration or distribution of Governor's permit money, but acting as a broker to maximize return to the states and provinces for their permits based on the network of bidders FNAWS has created over the years.

When it comes to maximizing revenue for donated permits, FNAWS is the best in the business. Supporting data for this statement come as the result of a dispute over allocating revenues from the Alberta permit in recent years. Disagreements with the recipient of the Alberta permit money (in Canada it must be an NGO) resulted in FNAWS not merchandising the Alberta permit at their 1999 convention. The Alberta sheep permit was auctioned at another major NGO fund-raiser, but the yield was only about 2/3 of the value the permit had been bringing at the FNAWS auction. This meant the anticipated potential, an additional revenue of $100,000 (US), was not realized for conservation.

The money FNAWS raises for Grant-In-Aid projects still comes primarily from donated hunts and other items (exclusive of the big-money Governor's permits), and is a considerably smaller amount. In addition to funding projects through the Grant-In-Aid program, a portion of this money goes to operate the Foundation. In this aspect of its operation, FNAWS is again the exception among typical NGOs. FNAWS has the lowest operating costs of any successful major NGO. Expenses are minimized by maintaining a Foundation staff consisting of an executive director and 6 full and part-time staff members at Foundation headquarters in Cody, Wyoming. The Cody staff takes care of everything from convention planning and management (i.e. fundraising), to membership services, coordinating political and legislative liaison with other NGOs and governmental agencies, and sales of FNAWS merchandise such as hats and shirts. All other Foundation officials volunteer their services.

What all this means is the Foundation's Grant-In-Aid program literally lives or dies by the annual convention fund-raiser (exclusive of Governor's permits). Over the last 3 years, there have been minimal funds available for Grant-In-Aid funding because the Foundation "died" at several relatively recent conventions. Specifically, because of bad fiscal decisions regarding conventions in Philadelphia, Nashville, Hawaii, and San Antonio, more money was lost than was raised. As a non-profit organization, FNAWS did not have a huge cash reserve. The Internal Revenue Service does not like to see large bank accounts held by non-profit corporations, and past FNAWS Boards have consistently decided funding sheep projects is more important than accumulating a cash reserve for the Foundation. What cash reserve existed was spent paying off the debts resulting from these failed conventions, and some debt remained.

Adding to the cash flow problem is the fact that it is extremely difficult for some Board members (all of whom believe passionately in more and better sheep hunting) to refuse a funding request if there is any way it can be met. My impression from sitting on the Board is that biologists and managers fail to appreciate how painful it is for the Board to say "No" to any request, no matter how strange it may be. If we've got it, we'll spend it on sheep. Building a large cash cushion had never been an objective for FNAWS before this fiscal crisis.

In summary, decisions by past FNAWS leaders put the Foundation at the brink of bankruptcy by failing to have consistently successful conventions. Recent conventions appear to have been highly successful, but much of the money raised has been spent in making and keeping the Foundation financially solvent. As a rule of thumb, when the FNAWS convention is in Reno, the Foundation makes money. When the convention is moved to another city, which seems to suit the membership occasionally, the Foundation is likely to lose money. The wonder of the system is that, through increases in fundraising by Chapters and Affiliates in addition to the "Governor's permit money," expenditures by states and provinces have been generally maintained or increased even though the Grant-In-Aid funding from the National organization has been low.

THE FNAWS ENDOWMENT FUND

Not having money to fund Grant-In-Aid projects was simply unacceptable to the FNAWS Board. Consequently, forward-thinking members of the Board conceived the notion of establishing an investment account to provide stable future funding.

The idea was to generate a huge pot of money (the final goal was $10 million) which would earn interest that could provide money for future Grant-In-Aid funding. Once this project was undertaken by the Boards that have shepherded its conception and development, another decision was made which further decreased traditional Grant-In-Aid funding.

The Board decided to minimize Grant-In-Aid funding to capitalize the investment fund as quickly as possible. Eventually, probably in half-a-dozen years, this "New Beginnings Trust" will provide a steady income sufficient to allow shotgunning of proposals as in the early days of the Foundation.

I'm still not comfortable with the "shotgun" or "blackmail" approaches to funding Grant-In-Aid projects (which I'll discuss later), but it is impossible to argue with the overall past success of the Foundation. Still, I think we, as a Foundation, and as professionals, can certainly do better than we have in the past. As professionals, we have a major responsibility in this regard. We have to think better, and offer more responsible proposals than we have in the past.

GETTING GRANT-IN-AID REQUESTS FUNDED

In the past, when Grant-In-Aid money was relatively abundant, many projects were approved simply because somebody said they would "put more sheep on the mountain;" and there was money available. This is no longer the case, but many professionals seem not to have caught on to the fact that times have changed. There is less money and much more stringent review of grant requests than in the past. At least some of this increased review rigor is my fault.

As a working sheep biologist, I'd written my share of Grant-In-Aid proposals and collaborated on even more. Hence, it is my conceit that I pretty well knew the grantsmanship game from the professional side. Once retired from active field biology, and prior to running for the FNAWS board, I began to review Grant-In-Aid proposals for FNAWS. I did this for 3 years.

During those years, the mechanism for proposal review was that proposals (usually about 50 per year) were sent to a panel of reviewers, upon which I served. These reviewers were to rate the proposal on a numerical scale based on their judgment of whether the proposal would "put more sheep on the mountain." The numerical ratings from the review panels were then forwarded to the Board to assist it in funding the most promising projects.

As a reviewer, I was frequently appalled by the casual approach to, and the low quality of, proposals for the limited Grant-In-Aid funds. Taking my responsibilities as a reviewer seriously, I typically wrote pages of comments for consideration of the FNAWS Board of Directors relating to the biological, political, and management soundness of these grant requests.

After being encouraged to run for the Board and winning election, I began to sit in Board meetings where Grant-In-Aid requests were evaluated, and the minimal available funds disbursed. As a professional, I was shocked to discover the difficulty the Board had in rejecting any proposals, even very weak ones. I was also surprised to learn that criteria other than biological soundness and management effectiveness figured prominently in whether a grant request was funded. I soon learned that part of "putting sheep on the mountain" is continuing to have success in raising funds to do so. This was assumed to require the occasional politically expedient funding of grants that held low potential to actually put any "sheep on the mountain" just to keep the money flowing into the Foundation through the traditional donated hunt mechanism.

As noble as the Foundation's goal is, and as much as it has accomplished through generating and disbursing money, it turns out that donors (as well as purchasers) are not completely altruistic. That is, many donors "invest" rather than "donate." *Certainly, there are many altruistic donors who actually sacrifice their best economic interests for the overall improvement of wild sheep, and I would not impugn their motives for an instant.* However, typical donors are humans who want something good to happen for them as a result of their donation. Artists want to become known, guides want clients in the future, guide/outfitter organizations want money spent in their region or province so their businesses will thrive, and even the most altruistic of FNAWS donors basically wants more and better sheep hunting. This is entirely appropriate. As stated above, this unabashed allegiance to the classic wildlife management ethos, providing human benefits through hunting, contributes to the unique character of FNAWS as a non-governmental organization. This fundamental value has, after all, been the foundation for the most effective conservation program the world has ever seen (Heimer 1999*b*).

Recognizing this tendency to maximize one's inclusive fitness explains what I half-seriously refer to as the "blackmail" component of project funding. As detailed above, donated hunts are still the life-blood of the FNAWS Grant-In-Aid program. Understanding that most humans involved in providing revenue for FNAWS are logically more interested in investing than in altruism helps understand why proposals which hold little promise of "putting sheep on the mountain" are occasionally funded, while biologically better proposals are rejected. Guide/outfitter umbrella organizations, as well as more than a few individual guides, will occasionally let it be known that if some FNAWS Grant money doesn't get spent to enhance sheep populations in their areas, donated hunts will "dry up."

Our responsibility as professionals (where FNAWS Grant-In-Aid funding is concerned) is to think better, write better proposals, and rely progressively less on "blackmail" and "schmoozing the Board at conventions" to get proposals funded. Our responsibility to the publics we serve as agency employees is to recognize our legislative and constitutional mandates with respect to wild sheep resources, and our responsibility to our agencies is to help them re-examine the assumptions upon which program priorities are established. If we discharge these responsibilities, we will have done well.

SUMMARY

The Foundation for North American Wild Sheep has proven, over the last quarter century, that it is certainly more than a group of "trophy-crazed sheep hunters." It has been intimately associated with, if not primarily responsible for the most striking wildlife conservation/ restoration success in the last quarter of the 20th century, the doubling of bighorn numbers in North America. The FNAWS role in this success has been considerably more than providing money. The unique FNAWS character has challenged, with variable success, the established paradigms of wildlife management priority, and may have established a beachhead for eventual recognition of sheep management as an important agency responsibility. One personal goal I have for the Foundation is to raise the status of wild sheep management in the corporate cultures of state and provincial management agencies so FNAWS can become a complete cooperator, in addition to a friendly adversary, and be respected as such by the agencies and their professional employees. FNAWS funding mechanisms have evolved from exclusive reliance on donated hunts to raise money for funding specific FNAWS projects, through the Governor's permit process which provides money for state and provincial discretionary funding for sheep programs, and future funding is anticipated from the "New Beginnings" trust account. There have been triumphs and failures, but for a small NGO (approximately 6,000 paid national memberships and up to about 15,000 more affiliate members in total), the overall performance of FNAWS over the last 25 years has been amazing.

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WORKING SESSION

Dealing with Unprecedented Levels of Aircraft-Supported Commercial Activities

MODERATOR: **Jeff Denton**

Panel Members: **Alasdair Veitch, Northwest Territories**
Kirby Smith, Alberta
Jon Jorgenson, Alberta
Bob Forbes, British Columbia
Jean Carey, Yukon Territory
Jeff Denton, Alaska

At the 12th Northern Wild Sheep and Goat Council symposium held in Whitehorse June 2000, a special workshop devoted to the topic of disturbance effects on wild sheep and goats was conducted. This workshop was hosted by Jeff Denton, an Alaskan biologist. The following is a collection of pre conference agency responses, panel presentations and notes taken by Alasdair Veitch, Jeff Denton, and several other attendees.

Many pristine northern wild sheep and goat populations and their habitats have experienced an unprecedented increase of aircraft-related activities in the last 15 years. Management agencies must deal with a wide array of permitting processes to deal with an ever-increasing number of applications for these activities. Research about the short-term physiological and behavioral response of wild sheep and goats is insufficient to evaluate current types and levels of aircraft activities. Long-term effects relative to habitat fidelity, population stability, and productivity are largely unknown when considering the permanent nature of many of the high volume long term aircraft operations being experienced today. Research studies of 1-3 year duration have been completed to evaluate short-term disturbance actions. However, few deal with the cumulative effects of long-term annually recurring high volume helicopter tourism, heli-skiing, and heli-hiking in addition to ongoing helicopter-supported mineral exploration and development, military missions and forest harvest.

Purpose

This workshop was convened to:

- Assess the status and scope of aircraft- related disturbances on North American sheep and mountain goats and the effectiveness of current mitigation and guidelines;
- Initiate a process to establish interim guidelines until further research can be done; and
- Initiate discussion about research needed to evaluate and develop consistent and adequate guidelines for permitting and regulating aircraft activities in sheep and goat habitats.

Regional Overview

Information was solicited from key personnel by questionnaire and telephone contact prior to the conference. Phone contacts were also made to give biologists the opportunity to prepare information and bring it to this session or forward it to the moderator for brief presentation. This was not meant to be a comprehensive account of the issue, but a representative sample to generate discussion. Questions asked were:

- What types of aircraft operations, intensity, geographic distribution, and temporal activity that occur in or near your sheep and goat habitats?
- Is there any ongoing or completed research investigating behavioral, physiological, habitat fidelity, short and long term productivity parameters in relation to aircraft activities?
- What is the prognosis for the future expansion or increase in aircraft operations or types of operations in the future? For example, Alaska has experienced rapid growth in activities aimed at the tour ship market (helicopter flight seeing and glacier landing operations, heli-skiing/snow-boarding, heli-hiking, heli-floating, para-gliding, ultra-light aircraft, etc.). Some of these activities are seasonal, others are year round and some are long term as well as short term, and of varying intensity.
- Are there any permitting requirements? If so, are there standards or stipulations for aircraft operators relative to distances, types of aircraft, noise levels, seasonal restrictions, etc.?
- In your region is there merit to having consistent and effective guidelines or stipulations for various aircraft activities whether it be mining logging, tourism or personal use related or of high intensity or limited in intensity frequency, and duration?
- Do you consider current or anticipated effects of aircraft operations on sheep and goat populations significant enough for the Northern Wild Sheep and Goat Council, as a professional group, to formulate interim and/or other more permanent management guidelines to deal with minimizing aircraft impacts, or do you consider each local situation as a separate issue to be addressed on a local basis?
- Are you satisfied with current management and see potential aircraft impacts as an issue that is already being adequately addressed?

Responses generally indicated that the potential conflicts in most of the western United States are not as intense as in Alaska, or are handled through special designations of land uses (such a wilderness areas), state wildlife agencies permitting, land use designations that limit helicopter use, or state statutes dealing with harassment. The degree to which the issue is addressed varies by state.

Submitted responses

Arizona

- Aircraft and stress in sheep is the most important area for study. The effects of stress on sheep demographics is a diffuse effect and difficult to study.
- Arizona has harassment provisions in a preliminary published form. There are no current codes or law structures that deal with general harassment.
- Currently special designations in some areas restrict aircraft uses and give some protection to sheep.

- Guidelines would be valuable for management agencies.

California

- California Fish and Game does not permit actions such as flying to set up hunts, or surveys, and requires FAA regulations to be followed. Flight seeing is allowed but not for the purpose of wildlife viewing.
- Many areas are federally designated national parks, monuments, refuges, or wilderness where helicopter uses are restricted by FAA designations and specific restrictions.
- There are no particular regulations or known conflicts with helicopters, ultra light aircraft or hang- and para- gliders.
- State wildlife harassment laws indicate flying within 60 m of wildlife constitutes harassment.

Colorado

- The only state regulations regarding helicopter use relate to the hunting, harassment or taking of wildlife with aircraft.
- Federally designated special areas such as National Parks, wilderness areas etc. and FAA regulations appear to be effective in most sheep and goat areas.

Idaho

- There are no state-applied guidelines.
- Specific research into military overflights in the California bighorn areas of southwestern Idaho has resulted in several resolutions and guidelines:
  - flight lines are to cross canyons at right angles and at a minimum of 1000 feet above canyon rims;
  - no flying in canyons;
  - 1000 foot flight limits over sheep habitat; but 10,000-foot flight limits for supersonic aircraft.
  - The degree to which these guidelines are adhered to in practice is unknown.
- The Sawtooth National Recreation Area deals with heli-skiing in a very controlled manner, based on very close cooperation among heli-ski operators, state, and federal agencies. Helicopters are required to stay 1000 feet above and one half mile away from goats and elk while transporting skiers to ski sites. Some areas are completely closed to all operations if Idaho Department of Fish and Game surveys indicate goats are present. Some areas are seasonally closed for wolverine natal denning after February 15. There is a reliance on the trust for the operator to comply, but some disturbance still occurs and monitoring is necessary. Permits are changed based on the monitoring and observations made over the previous 5 years.

Montana

- Guidelines were established primarily in response to oil and gas exploration activities and might be considered out of date.
- The Montana Chapter of the Wildlife Society completed a review of the effects of recreation on Rocky Mountain Wildlife in 1999; however aircraft based recreation was not evaluated.
- There is some heli-skiing near Glacier National Park. Helicopter related recreation may be occurring in other areas but has not become an issue or has not come to the attention of the

state wildlife agency.

- Interagency guidelines were developed during 1980-1987 for the Rocky Mountain Front to meet a number of objectives, including mountain goat and bighorn sheep management.
- Specific guidelines for mountain goats and sheep relative to helicopters and aircraft in Montana:
  - Seasonally avoid areas:

Kidding-nursery areas - mountain goat	May 1- July 15
Lambing areas - sheep	April 15-June 30
Breeding areas - mountain goat	November1- December 31
Winter Range - mountain goats	October 15 - May 15
Winter ranges and breeding areas - sheep	September 1 - May 15

  - Survey suitable habitats and classify as yearlong or transitional habitat. Year long habitats will have the seasonal guidelines apply and transitional habitat will have human use restrictions May 1 - June 30 and October 15 - December 31.
  - Mineral licks should have a no surface occupancy for a 1-mile radius around the site and helicopter flight patterns should be established at least one mile from mineral licks May 1-July 31.
  - Establish flight patterns when helicopter activities are required. Flight patterns should avoid seasonally important mountain goat habitat during the period noted above.
- These guidelines are for consideration when dealing with various activities and are not mandatory. They are often included in mitigation or stipulation packages dealing with various permits or authorizations. Monitoring of these guidelines was identified as an important test and validation of their effectiveness and applicability.

New Mexico

- State regulations are referenced to hunting statutes only.
- Federal land use designations protect many of the at-risk wildlife populations.

North Dakota

- Aircraft-caused disturbance within bighorn sheep range in North Dakota is currently at a minimal level.
- The United States Air Force (U.S.A.F) used to conduct low-level training flights with bombers and fighter jets over an area used by bighorn sheep. Flights were approximately weekly during the summer 1992-1994 (Sayre 1997). Sheep response varied from no reaction to increasing time spent alert to fleeing up to 1000 m away from the disturbance. Currently, the U.S.A.F. does not conduct these flight exercises.
- The North Dakota Game and Fish department conducts low-level aerial surveys of designated study areas during the spring and fall of each year. A single fixed-wing plane is used to survey 10-15-mi^2 study areas (60-90 minutes for each area). Mule deer and bighorn sheep are counted and classified during these aerial surveys. Big game biologists opportunistically aerially monitor bighorn sheep areas throughout the year. No other aircraft disturbance appears to be impacting bighorn sheep in North Dakota.

Sayre, R. W. 1996. Ecology of bighorn sheep in relation to habitat and oil development in the Little Missouri Badlands. Ph.D. Dissertation. University of North Dakota, Grand Forks, North Dakota, U.S.A.

Oregon

- In most cases wilderness designation precludes the type of aircraft operations that would potentially impact sheep and goats.
- Interim guidelines and longer term, research-based guidelines from a professional sheep and goat biologist/manager group would be useful in potential conflict areas.
- State regulations deal mostly with hunting and transport via helicopters for illegal taking of wildlife.

Washington

- Echoed for the most part, the Oregon response. State law also relates to the issues of same day airborne hunting.
- Research in the areas of intensive recreation and tourism impacts (on the ground and in the air) should be among the top priorities in sheep and goat management.

Presented responses:

Alaska (Jeff Denton)

- Aircraft related activities have experienced unprecedented expansion into previously pristine mountain goat and sheep habitats over the last 10-15 years. This expansion also includes increased intensity, duration, frequency, variety and long-term permanency of a variety of aircraft-related activities.
- The most prolific and visible increase comes from the high-volume tourism industry. This industry utilizes multiple-transit tours starting with the tour ships and uses buses, trains and commercial airlines to complete various tour circuit packages that include Ketchikan, Sitka, Juneau, Haines , Skagway, Glacier Bay, Valdez, Cordova, Seward, Anchorage, Denali, etc.
- Helicopter-supported skiing, snowboarding, hiking, rafting, kayaking, dogsled glacier tours; para-gliding, and ultra-light aircraft are currently experiencing an increasing demand for use. These activities are additive to the more traditional individual fixed-wing recreational flights for hunt scouting trips, helicopter-based logging, mineral exploration and development. All activities include wildlife viewing as an added benefit. They occur primarily along the coastal mountains in southeast Alaska, mainly on the Tongass National Forest with operations also occurring on State of Alaska and Bureau of Land Management (B.L.M.) lands in the Haines/Skagway and Anchorage areas. Operations in and around Denali, Glacier Bay and Kenai Fiords National Parks are also popular.
- Timber, oil, and gas-related activities are also increasing, but historically activity levels fluctuate with the economy.
- There are conflicting views among the outfitter community and the research community about the impacts of the Alaska pipeline.
- Long-term outfitters and guides have strong feelings that helicopter flight-seeing and other operations have had significant impacts on Dall sheep in their areas. These impacts are frequently related to sheep distribution and seasonal habitat fidelity, abandonment of habitats, significant impact on hunter success and sheep population stability.

- Intensive helicopter logging has been implicated in the loss of local goat populations in the Cordova and south-central Alaska regions. This is directly related to crucial habitat alteration and elimination. How much of the impact related to helicopter operations is not known.

Permitting

- The State of Alaska Department of Natural Resources has no permitting process for or monitoring of these activities. Distribution, intensity, and seasonality of these activities are largely unknown on state sheep and goat habitats. Monitoring these activities is difficult; some of these activities occur or expand into new areas without the knowledge or authorizations required by agencies on their respective lands.
- The number of permit applications is increasing rapidly each year – most are for flight seeing and include glacier landings, wilderness education, and skiing. Most are helicopter- supported and active primarily May through September. Increasingly, there are late winter seasons of activity in March-May for heli-skiing and other helicopter-related activities in many of the same areas mentioned above, as well as around Cordova, Valdez, and Kenai Peninsula state lands, B.L.M. lands, and Chugach National Forest lands.
- The Tongass National Forest currently permits up to 31,000 flights and landings per year on the Juneau Icefields, with an approximately additional 10% more flights for just point-to-point tours. Similar intensities are experienced in Ketchikan, Sitka, and other areas in southeast Alaska.
- Permit applicants indicate a demand in the Juneau Icefield alone for up to 40,000 flights and landings. Between B.L.M. and Tongass National Forest the Haines/Skagway area has about 7,000 glacier takeoffs and landings in a 150-day season from May 10 to September 30, plus an unknown number on state-owned lands and for winter heli-skiing activity. I do not have figures for other regions of the state where these activities occur, but they are probably significant in number and growing but not yet to the levels being experienced in the southeast.
- There appears to be a high interest and use in south central Alaska for heli-skiing.
- The tourism industry engages in, promotes, and vigorously protects aircraft-based tourism in the interior of Alaska and at major tour stops. The prognosis is that these types of tourism and recreation will increase and expand readily into new areas in the future.
- There has been research of at least one population of sheep with considerable exposure to aircraft operations and other intrusions. No specific research has been directed at the issue, but some experts indicate that aircraft impacts on this population of sheep may not be significant and that sheep can habituate or tolerate intense air operations in their habitats.

Monitoring

- U.S. Forest Service has no monitoring.
- Alaska Fish and Game only monitors at the levels needed to meet the needs of harvest management.
- The Park Service is not doing monitoring related to aircraft operational areas.
- B.L.M receives 3% of the fees associated with helicopter operation permits for monitoring. B.L.M has been monitoring mountain goats in the Skagway/Haines area since 1995. Monitoring occurs in an area where goats are exposed to helicopter activity and in a control area that is about 3 times the size of the exposure area. Major objectives are to monitor habitat seasonal use, area fidelity, productivity, population stability, and response behavior. This is not research-intensity monitoring, but is of sufficient intensity to detect developing

"red flag" situations that hopefully would trigger more intensive research efforts or modification of current permitted operations. The constant expansion of activities and types of uses into the control areas partially compromises the control area, but also allows for before, during and after comparisons of test areas. The data have not yet been analyzed, but some preliminary information is available:

  - 1995-1998: exposure areas and control areas have population demographics that were very similar from year to year. Long term (since 1985) exposure areas had stable, but very low and inconsistent productivity.
  - 1999: severe winter weather. Helicopter tourism/glacier landing exposure area suffered significant failure of reproduction and population decline whereas control areas stayed about the same as the previous 4 years. There is a possibility of cumulative stress from pre-winter tourism activities resulting in enough of a body condition deficit that harsh winter stresses resulted in at least a one season reproductive failure and adult mortality above that experienced in control areas. There appears to be declines or abandonment in use of kidding areas adjacent to landing sites in at least one situation. There are many possible explanations; analysis and probably more intense research is needed.

- On lands managed by Alaska Department of Natural Resources only FAA rules and State wildlife harassment laws are in effect.
- Compliance is, at best, expensive and difficult to enforce due to lack of manpower; non-compliance with permit stipulations, flight corridors, and landing sites is commonplace. Human flight safety takes precedence over wildlife stipulations whenever conditions are considered necessary. This allows a convenient scapegoat for deviation from established flight patterns, use areas, and so on.
- Since 1995, B.L.M. has required 1500-foot horizontal and vertical distances from wildlife habitat, based on limited research and general consensus of state and federal biologists at the time.
- FAA regulation and designations over special areas of Parks and Refuges, National Forests are available but largely disregarded in Alaska. The current feeling is that these are not adequate stipulations to protect mountain goats.
- The heli-tour industry is a well-connected "big-dollar" industry. Stipulations for seasonally protected kidding areas were eliminated via political routes.
- Agency decision-makers are often reluctant to apply mitigation or stipulations without multi-agency consensus and adequate research findings. The lack of comprehensive research, the political and economic climate, and the lack of interagency agreements or guidelines make effective and consistent decision making difficult.

Northwest Territories (Alasdair Veitch)

- In the northern part of sheep range (Richardson and Mackenzie mountain ranges) there are no year-round roads, although some areas are accessible by seasonal roads. There are no human settlements and currently no operating mines or forestry activities.
- Potential sources of disturbance are hunters (up to 350 per year and active from 15 July to the end of September), backpackers, river rafters, canoeists, kayakers, and, along major waterways, jet boats. There is 140,000-km2 total area, but there are 'hot spots' for human activity.

- Outfitters in the Ft. Liard area near the British Columbia border expressed concern in 1999 about helicopters (212s) flying low over lambing and post-lambing areas and blasting for seismic work occurring right at base of lambing cliffs. In 2000 Department of Natural Resources and Economic Development will survey to see if sheep are present in areas proposed for seismic activity. Seismic activity is currently only in the summer.
- Proposals for seismic work in areas with no settled land claim have to be screened by the federal National Energy Board (NEB). Applicants need a Geophysical Operations Permit issued under Canada's *Oil and Gas Operation Act*. The Government of Northwest Territories (Department of Resources, Wildlife & Economic Development – divisions Wildlife and Fisheries; Environmental Protection; Forest Management; Minerals, Oil, and Gas; Parks and Tourism) provides input during screening along with other stakeholders such as aboriginal organizations. The screening report goes to the Mackenzie Valley Impact Review Board and they decide if a permit is issued or if an environmental impact assessment needs to be done.
- In areas with settled land claims, Land and Water Boards issue land use permits and water licences for all lands, both private and crown. The Department of Indian and Northern Affairs Canada also looks at proposals.
- No disturbance studies are underway but the Gwich'in Renewable Resources Board may initiate studies to look at the impact of snowmobile disturbance on Dall's sheep in the Richardson Mountains.
- There are no federal or territorial minimum flight height guidelines. The only area where there are guidelines is the Inuvialuit Settlement Region in northern NWT; these guidelines are for caribou: 300 m above ground level for ferry flights; 100 m above ground level for survey flights. The NWT Department of Natural Resources recommends 300 m for Dall sheep overflights and 100 m for survey work.

Alberta (Kirby Smith)

- There are two main disturbance issues or problems: domestic dogs and overflights.
- Disturbance studies began with Val Geist, who had heart rate monitors in bighorn sheep. An article was published in the Journal of Wildlife Management in 1982. In 1995 Steve Cote looked at helicopter based seismic line activity and mountain goats (single line seismic activity with 206s and 212s) and published a paper in the Wildlife Society Bulletin in 1996. He detected disturbance to goats at 1500 m and recommended a buffer of 2000 m (i.e. 2 km) for helicopter activity in vicinity of mountain goats.
- Wild sheep seem to habituate to disturbance more than goats.
- Sheep hunters in Alberta complain about helicopter harassment. There is some talk about them suing government because of this.
- 1 seismic line = 120 overflights by helicopters; a project usually will have many lines.
- When 3D work is involved – lines are spaced at 400-m intervals.
- Seismic exploration using 3D methodology is very difficult to plan for because everything is kept confidential. Sharing information is not encouraged. In Alberta, if a company wants a 6000-m deep hole, then they also want 6000-m radius area <u>around</u> the hole.
- In April 2000 a meeting was held to discuss ungulates and seismic activity work. A 2-km buffer around mountain goat habitats was recommended to industry/government.
  - Guidelines were circulated within the Department. Industry was consulted. Staff met

with industry and showed them the recommended guidelines (contact Kirby Smith for copy of: *Operating Guidelines for Industrial Helicopter Activity in Mountain Goat and Bighorn Sheep Ranges in Alberta.*)

- Key principles:
  - These guidelines are ok for geophysical work but make every attempt to avoid heli-portable operations if at all possible.
  - Overflights are restricted to no more than 2 flights/day
  - Apply a 2000 m 'no fly zone' around identified mountain goat and bighorn sheep range
  - Use ground-based techniques wherever possible
  - Transport geophones by backpack or horse wherever possible
  - Start after 01 July and go to 22 Aug (7 days before hunting season). This gives companies 7 weeks to work
  - Overflights to stay over 200 m above ground level above alpine areas
- Industry response: "we agree with everything but want to still use helicopters." Prognosis on effectiveness of implementation is an expectation of non-compliance. Bottom line is we will have to use the use the *Wildlife Act*: essentially give them a permit, and then charge them with harassment when they start work!

- Goat monitoring research is ongoing at Caw Ridge. Data regarding yearly weights, reproductive performance, numbers of goats, sex of known-age goats is collected. We use the same categories as Steve Cote did with his work. GPS transmitters on helicopters provide information on where the machine is relative to sheep and goat habitats every 5 minutes. We can then quantify disturbance.

Alberta (Jon Jorgenson)

- The problem of disturbance is recognized in Alberta. It is growing from 2 sources: commercial tourism use of helicopters and oil/gas exploration activities.
- Except for some protected areas (National Parks, Provincial Parks, etc.) where there is legislation governing landings, there is nothing to prohibit overflights or to deal with landings. We therefore have to deal with guidelines and develop these in association with industry. We have done this for some areas in the province.
- Helicopter-based tourism has rapidly increased since 1988, but is localized primarily in the Canmore area near Banff National Park.
  - Helicopter-based tourism industry started in the late 1970s.
  - Canmore heliport was built 1989. There are 7-8 helicopters based in Canmore all summer (A-stars and Bell 207s).
  - May to early September is the current operating season; about 6000 helicopter overflights occur during this period.
  - The main concern is mountain goats – we have small populations in restricted ranges. These small isolated populations are now easily accessible islands exposed to heli-hiking, heli-biking, and heli-barbecuing, among other things. Lots of people are going into goat range. There doesn't seem to be much of a concern elsewhere right now, but this could easily change as applications for other areas and for different seasons of use such as heli-skiing are increasing.

    - Success currently is due to naive applicants; guidelines and education are reasonably successful, but there is a need to get and keep on top of it. The problem is that there are few legal options because wildlife management agencies have no control of airspace. There is only one case noted where an area was closed – that being during 1988 Winter Olympics and was more for security reasons during the Olympics than wildlife related issues.
- We have had meetings with helicopter companies to attempt development of voluntary guidelines. The resulting guidelines were primarily based on Steve Cote's work:
    - fly a minimum of 2000 m from occupied goat habitat; 1300 m from sheep habitat
    - identify sheep and goat seasonal and sensitive habitats (includes obtaining good data on seasonal ranges, kidding and lambing habitat areas, etc.) within the sphere of operations for helicopters. Put seasonal constraints around sensitive habitats and some year-round constraints. Kidding periods are considered critical habitats for protection.
    - these guidelines came into effect in 1999. We are now are monitoring to see how well (or if?!) they are working
- Goat populations have been reduced within areas being overflown, but we cannot conclusively say it is due to helicopter-related disturbance. Also, elk have vacated the overflown areas.

British Columbia (Bob Forbes)

- There are concerns about snowmobiles, quads, four wheelers, tracked vehicles etc., but most concerns center around helicopter tourism operations, specifically heli-hiking and heli-skiing in Southeastern British Columbia.
- The activity is growing very rapidly and it is a new realm for us, as we have never before considered the impacts and stresses of recreational activities. Past research has not focused on impacts of tourism and the many forms that tourism and recreation can take.
- Industrial helicopter operations are an issue but a lesser one.
    - In 1996 the British Columbia government implemented a backcountry use policy. Once companies had to apply for a licence, the Wildlife Branch was alerted to the number of licences being applied for and recognized that a year-round problem existed on a widespread scale. The issue is a hot topic now.
    - Companies believed they were being eco-friendly by being tourism-based and advertised themselves as such. However, they were not sensitive to sheep and goat habitats and protection needs. The Wildlife Branch tried, unsuccessfully, to educate companies about the real impacts of such activities.
    - 85% of Crown land in southeastern British Columbia is being sought by heli-hiking/heli-skiing companies.
    - When maps of heli-tourism operations were overlaid with sheep and goat population distribution maps, 'soft' correlations were observed with goat declines; however there are lots of other issues and potential impacts.
- The Wildlife Branch started a review of disturbance impacts, pulled the literature, contacted other management jurisdictions and arrived at the following common ground conclusions:
    - most jurisdictions are concerned about heli-based recreation and tourism operational impacts
    - There are no management guidelines in place in other jurisdictions

- There is little ongoing research that addresses the specifics of the issues
- Others were waiting for the Wildlife Branch to do something and said, "when you get some guidelines, let us know because we'd like to implement some guidelines too..."

- In 1997-98 the first regulatory policy and management guidelines were established based on work in Alberta by Steve Cote. These include:
  - Mountain Goats- 2000 m no-fly/no-land buffer around designated goat habitats
  - The 2000-m zone guidelines caused a fight with operators because this reduced flying areas to as little as one-quarter of the area they formerly used. This conflict lead to draft guidelines to be applied to operations in 2000 that include the following:
  - Mountain Goats: 2000 m horizontal and vertical distance no fly/no land buffer
  - around designated mountain goat habitat
  - Mountain Sheep: 1000 m horizontal and 500 m vertical distance avoidance buffer around designated sheep habitat
  - Designated goat and sheep habitat is identified by Wildlife Branch.
  - Timing restrictions for critical life cycle habitats such as lambing/kidding. Timing restrictions appear not to be nearly as controversial as avoidance restrictions.
- Many operators are illegal relative to these guidelines.

Yukon Territory (Jean Carey)

- Currently helicopter tourism use levels are incidental. The Yukon doesn't have nearly the volume of tourism flights as southeast Alaska.
- The Yukon Department of Renewable Resources encourages helicopter access for mineral exploration so that we don't see a greater push to build more roads. Most types of exploration activity do not require permits.
- When permits are required, we appear to have 'won the battle' to restrict flying near lambing cliffs 1 May – 15 June. Currently use a 1500-m setback distance, but recent research suggests that this should be increased.
- We are counting on corporate goodwill – that companies want to be seen to be doing the right thing. It is a risk management situation at this time.
- There is insufficient information and a pressing need for real data to establish adequate guidelines. In 1996 a literature review was done, a study design was developed, and a research project was initiated. Results of 2 of these studies are included in these proceedings.

Summary

It appears that the potential impact of helicopter-based commercial recreation is recognized as a management issue primarily in Canada and Alaska. It is apparent that each jurisdiction and agency is making some attempt to address the issues. There is a lack of consistency between state agencies and federal agencies within the same geographic areas although there appears to be some cooperative effort. The lack of sufficient short- and long-term research findings and true tests of existing guidelines hinders the development of solid guidelines. Guideline compliance by commercial operators is based on good faith because of the difficulties and expense of monitoring activities. Overall, compliance appears to be inadequate except where extensive cooperative efforts are made.

It appears that mountain goats are more sensitive than sheep to helicopter-supported operations. However, much is not known and the variations among populations and habitats are not well understood. To direct research and develop guidelines of merit, it is imperative that we thoroughly review what is known, determine what specific research is needed, and develop and implement conservative general guidelines and specific considerations for managers. When research yields the data, specific and adequate guidelines can be drafted to guide this expanding industry. It appears that British Columbia, Alberta, and Montana have taken great strides in establishing initial guidelines. All jurisdictions have considered the issue and can contribute to adaptive management guidelines and advance the research base from which to make valid long-term guidelines.

Comments and Discussion

Wayne Heimer (Alaska)

Dry Creek study area about 60 mi. from Denali National Park

- Helicopter tourism activity.
- High-density sheep population w/ low reproductive rate.
- Geological drilling/prospecting supported by helicopters.
- Fixed-wing aerial surveys by Alaska Dept. Fish and Game.
- Also snowmobile activity and high density wolf predation.
- No heli-skiing or heli-hiking.
- Compare demographic data from here with Dall's sheep in Denali National Park. – no differences.

Mr. Heimer suggests that biologists have to examine their assumptions and biases – we biologists don't like to see people in 'our country'

Dale Toweill (Idaho)

- They "studied sheep to death" and there is a need to evaluate the cost to the resource in order to validate our position.
- In Idaho, military ranges are good for sheep because they keep out cabins and so on.
- Should we have 'sacrifice areas' where snowmobile or heli-tourism or other activity is ok in order to have other areas 'off limits' to these activities?

Charles Jurasz (Faro, Yukon)

- There is tremendous amount of information available on this issue.
- Sound frequency is important and significant. We need to know the frequency at which a lamb responds to noise versus that which a ram responds, as they are not necessarily the same. Look at the body of literature available for marine mammals and interference frequencies.
- Need to look for the weaknesses in the models we create.
- Harassment equals taking.

Steve Gordon (British Columbia)

- Cote recommendations rejected by B.C. Forest Service.
- 500-m horizontal distance now used instead.
- 01 May to 31 October – window during which activity is allowed to occur.

- Weather precludes activity for most of the year except summer.
- Helicopter logging goes against even the recommended 500-m distances.
- B.C. is looking for a position paper from the Northern Wild Sheep and Goat Council.

Kevin Hurley (Wyoming)

- Heli tourism picking up in the Tetons but is not as bad as in other areas.
- Oil and gas activity has increased substantially over the last 5-8 years.
- Heli-portable seismic activity is the main concern.
- Recommended that this activity occur in summer so that public can see what is happening.

Glenn Erickson (Montana)

- Montana has guidelines, but they are now out of date.

Michelle Bourassa (South Dakota)

- Badlands National Park gets helicopter overflights.
- No recommendations for tourism. Companies usually fly 700-1200', using 4 flight routes.
- Has been monitoring sheep for 3 years, and has not noted any visible reaction to helicopter overflights.

Jeff Denton (Alaska)

- There seems to be a difference among populations in terms of habituation.
- In most agencies the people who make the decisions are not biologists.
- There needs to be more than just one biologist telling the decision-makers what needs to be done. Looking for interim guidelines from NWSGC to take back to his agency.
- reiterated need for NWSGC to develop guidelines and need to address those to policy makers

Jim Karpowitz (Utah)

- In the Moab area the movie industry is a bit of a problem. B.L.M is trying to control the industry a little, but movie folks then just move onto private and state lands.
- Tried to transplant some sheep adjacent to a bombing range – they were turned down.
- Disease problems attributable to disturbance-related stress? Don't know, but are concerned.

Alasdair Veitch (NWT)

- Did experimental study of effects of jet fighter and fighter/bomber low-level flights on woodland and barren-ground caribou in Labrador for 3 years. Exposed cow caribou had decreased calf survival, but mechanisms are unknown. In terms of short-term behavioral responses – low flying helicopters caused caribou to react much more than low flying military jets. Did not see movement of collared cow caribou out of flight corridors approved for military low-level flying. Has 2 papers published on the results of this experimental study. People interested should contact Alasdair and he will send reprints.

Jean Carey (Yukon)

- We need to look carefully at what any NWSGC guidelines will be based on. Need to document guidelines with research. Do we have the data to make a generalized model?

Dale Toweill (Idaho)

- We had a 10-year negotiation with Pentagon. If we spend time documenting research – industry wins. Need general guidelines for all situations and then generate specifics for each particular situation.

Kirby Smith (Alberta)

- we need a literature review initially for both sheep and goats

Wayne Heimer

- Near a semantic quagmire. What is a guideline versus what is a stipulation? Has no problem with guidelines. Stipulations lead to regulations, permits, etc.
- Gradual is better than sudden.

Don Whittaker (Washington)

- Mule deer group has a model for predation. First did a literature review to pull all the information together – lots of stuff with agencies.
- We should have someone pull all the info in this area together into a synthesis of what we currently know.

Jeff Denton

- Have a committee to synthesize this information.
- Will be putting a paper together for the proceedings of this conference

Kevin Hurley

- 3 steps:
    - capture all the information on what's going on with a literature review
    - generate some generalities that we can all agree on
    - identify research that is needed

Jean Carey

- Yukon Territory Government has sheep/disturbance literature review that was up-to-date as of 2-3 years ago. Have the same for mountain goats done by Kluane National Park.

Dale Toweill

- has some classified stuff from the Pentagon

Michelle Bourassa

- Is interested in disturbance along roads. Is anyone else interested in this?

Participants interested in being on a committee:

Michelle Bourassa
Mari Wood (BC)
Dale Toweill
Jean Carey
Charles Jurasz
Kathreen Ruckstuhl (Alberta)

Lydden Polley (University of Saskatchewan)

- In the review article that this committee is planning/proposing to put together, it is imperative that it be very careful in judging the quality of the research. This is not a trivial matter.

At this point a committee was struck. Jeff Denton will coordinate things and prepare a document for proceedings.

End of Workshop

Biennial Symposium Northern Wild Sheep and Goat Council 12:153-169.

FLEEING DECISIONS BY DALL'S SHEEP EXPOSED TO HELICOPTER OVERFLIGHTS

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Abstract: I asked whether Dall's sheep (*Ovis dalli dalli*) disturbed by helicopter overflights made fleeing decisions that were consistent with economic models of prey fleeing from predators. Agreeing with these models, fleeing probability decreased as the helicopter's approach became less direct, but the rate of decrease was greatest when sheep were on rocky slopes, which are a refuge from cursorial predators. Furthermore, sheep >20 m from rocky slopes always fled, even during indirect approaches, and distance fled increased with distance to rocky slopes. Approach directness affected fleeing probability only on a horizontal plane possibly because trials in which the helicopter was far above or below sheep were few. Contrary to predictions, flight initiation distance decreased with the horizontal component of approach directness. The latter, however, is geometrically correlated with the sheep's minimum horizontal distance from the helicopter trajectory, and flight initiation distance was largely determined by animals fleeing when the helicopter reached its nearest point to them. Flight initiation distance also increased with group size and distance to obstructive cover, suggesting lower perceptual constraints in groups of greater size or farther from obstructive cover. While sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and do not warrant the energetic costs of antipredator behavior, I found no evidence of habituation. Results provide preliminary parameters for models predicting energetic and fitness costs incurred as a function of overflight rates. Guidelines to mitigate disturbance could be created using logistic regression models of fleeing probability predicting the minimum distance from trajectory (a geometric correlate of approach directness that is controllable by pilots) causing acceptably low disturbance rates.

Key words: approach directness, conservation biology, Dall's sheep, distance to refuge, fleeing decisions, group size, helicopter disturbance, obstructive cover, *Ovis dalli dalli*, predation risk

Prepared for the Yukon Fish and Wildlife Branch, Department of Renewable Resources, Whitehorse, Yukon. Revised November 1999.

Predation risk and human disturbance have similar effects on animal behavior. Both can limit access to resources (Gilliam and Fraser 1987, Cameron et al. 1992, Gill et al. 1996), cause greater vigilance (Stockwell et al. 1991, Frid, 1997), and elicit fleeing (Ydenberg and Dill 1986, Bleich et al. 1994, Côté 1996). These responses create energetic costs that may affect reproductive success. Thus, economic models of antipredator behavior predict that prey should maximize fitness by making optimal decisions that consider the trade-off between energetics and safety (e.g. Ydenberg and Dill 1986, Lima and Dill 1990).

Consistent with these models, prior studies have predicted and found that the probability of prey fleeing and their distance from the predator at which they begin to flee increase when predators (as simulated by humans) approach more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998; see Bulova 1994 for an exception). These responses might occur because a direct approach indicates that the predator has detected the prey and intends to capture it (reviews in Cooper 1997, 1998). Flight initiation distance and distance fled from a predator have been predicted and found to increase as distance to refuge becomes greater. This response is attributed to risk of capture increasing with distance to refuge (Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova, 1994, Kramer and Bonenfant 1997). The effect of group size on flight initiation distance is more difficult to predict because more sensory organs reduce perceptual constraints (i.e., larger groups might detect a predator when it is farther away), and group size therefore may be positively related to flight initiation distance. Larger groups, however, also dilute the individual's risk of predation, and flight initiation distance may be negatively related to group size (Ydenberg and Dill 1986, Dill and Ydenberg 1987). Not surprisingly, both positive and negative effects of group size have been observed (review in Ydenberg and Dill 1986).

Unlike prey facing predators, mountain Caprinae disturbed by helicopter overflights do not risk direct mortality. Still, these animals often behave as if helicopters were threatening by fleeing, increasing vigilance, and switching habitats (Stockwell et al. 1991, Bleich et al. 1994, Côté 1996). Thus, unless mountain Caprinae learn that helicopters are not a threat to life, they should treat the decision to flee from them as a trade-off between predation risk and energetics (see Ydenberg and Dill 1986). Prior research on helicopter disturbance, however, did not consider this hypothesis.

In this study I test whether fleeing responses by Dall's sheep (*Ovis dalli dalli*) exposed to helicopter overflights are consistent with economic models and observations of prey fleeing from predators (e.g. Ydenberg and Dill 1986), and discuss the conservation implications of my results. I predicted that fleeing probability, flight initiation distance, and distance fled would decrease as the minimum distance between sheep and the helicopter's trajectory increased. The basis for this prediction is that minimum distance from trajectory is geometrically correlated to the plane's three-dimensional angle of approach, with a shorter distance implying a smaller angle and a more direct approach (Burger and Gochfeld 1981; 1990; Bulova 1994; Cooper 1997, 1998). I focused on the horizontal plane of approach directness because the helicopter's elevation relative to sheep had limited variability (see Methods). I controlled statistically, however, for the effect of relative elevation.

My second prediction was that fleeing probability, flight initiation distance, and distance fled would be directly related to distance from rocky slopes. Rocky slopes are a refuge from cursorial predators for sheep (Berger 1991; review in Frid 1997), and sheep may be less responsive to any threatening stimuli while near or on rocky slopes (see Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova 1994, Kramer and Bonenfant 1997). Also, I expected that sheep not on rocky slopes would flee towards them.

In addition to testing the above 2 predictions, I assessed the effect on fleeing decisions of group size and obstructive cover. Group size could be related to risk dilution and/or perceptual constraints, while obstructive cover is related to perceptual constraints only (Ydenberg and Dill 1986, Dill and Ydenberg 1987). I assessed also whether approach directness by the helicopter combined multiplicatively rather than additively (i.e., interacted) with group size and/or distance to rocky slopes to affect fleeing decisions. The rationale for analysing interactions was that prior studies have found that the antipredator response by prey exposed to a given risk factor may depend on the level of risk created by other factors (e.g. Burger and Gochfeld 1981, 1990; Frid 1997; Kramer and Bonenfant 1997, Cooper 1998).

Finally, I predicted that sheep would become more tolerant of direct approaches by the helicopter as weeks of cumulative overflights increased. Predicting habituation is within the framework of economic models of predator avoidance because sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and therefore do not warrant the energetic costs of antipredator behavior (see Burger and Gochfeld 1981, 1990).

METHODS

Study sites, animals, and season

I collected data between mid-June and early August, 1997, in the southwest Yukon Territory, Canada. I made 49 observations at Hoge Pass (ca. 61 °19' N, 139° 33' W), Kluane National Park Reserve (KNPR), 6 observations at Nines Creek (ca. 61° 11' N, 138° 50' W), Kluane Wildlife Sanctuary, and 1 observation at Vulcan Creek (ca. 60° 55'N, 138° 29' W), KNPR. All sites contained >200 sheep, were roadless, rugged, and harboured large carnivores.

At the principal study sites (Hoge Pass and Nines Creek), fixed wing and helicopter traffic occurs mainly between May and September, perhaps averaging 25 flights per season for each aircraft type (not including flights related to my studies), but precise records are lacking. I collected 88% of observations at Hoge Pass not because helicopters threatened sheep there, but because that site provided excellent observation conditions.

I pooled observations of female-young groups (N = 38) and all-male groups (N = 18) to maximise sample sizes. In pooling reproductive classes, I chose to gain statistical power at the cost of potential increases in unexplained variability. I assessed, however, whether pooling the sexes was justified in analysis of fleeing probability (see Results.)

Experimental disturbance and recording behavior

Sheep were exposed to overflights by a single helicopter (Bell 206B) flying at a mean ± SD air speed of 165 ± 31 km/h. At Hoge Pass responses to disturbance were tested experimentally; I designed a priori and communicated to the pilot (via radio) the helicopter trajectory. At Nines Creek and Vulcan Creek, overflights were related mainly to mineral exploration and data were collected opportunistically.

My assistants and I observed sheep from the ground, from distances of >1 km and using spotting scopes and/or binoculars. We simultaneously observed 1-4 focal groups (1/observer), and recorded continuous sampling of their behavior (Martin and Bateson, 1993) into tape recorders. These records started several minutes prior to overflights and continued until animals stopped reacting. Female-young groups tend to be large, and often we could not observe all group members at once. Thus, I quantified the timing of responses based on the behavior of the first animal or animals to respond in the group (most responses involved >50% of the group, see Results).

Recording aircraft trajectories and sheep locations

In 45 of 49 observations at Hoge Pass (80% of data for all sites), the pilot obtained the helicopter's position in relation to time during the observation period using a GPS system. Specifically, he communicated his position and speed via radio 2-3 times per minute to observers on the ground, who recorded data directly from the radio into a tape recorder which was activated at the onset of the observation period.

For all trials at Nines Creek, the 4 observations for which the helicopter GPS was unavailable at Hoge Pass, and the one observation at Vulcan Creek, the helicopter's position in relation to time during the observation period was recorded as follows. An observer picked a priori distinct points in the landscape, and numbered them on the 1:50,000 map. When the helicopter flew over these points, he spoke the number identifying them into a tape recorder which was activated at the onset of the observation.

Sheep locations were plotted shortly before beginning behavioral observations using compass bearings and 1:50,000 topographic maps. After field work, the helicopter's positions (each corresponding to a given second in the observation period) were transcribed onto the maps containing sheep locations. Spatial variables involving the sheep's location and/or timing of sheep behavior in relation to the helicopter's position were measured from these maps. Helicopter positions that were not obtained from the pilot that were needed for analyses were estimated from known positions and the helicopter's speed.

I used the 1:50,000 topographic maps and known points on the landscape to estimate the sheep's distances to rocky slopes and obstructive cover (defined below), and the distances fled. When distances were <100 m, however, estimates used torso lengths of adult sheep (representing approximately 1 m) as reference points.

Distances were measured from the "average" center of the group. In other words, when most group members were at a core area but there were also outlying group members, measurements were made from a point that was shifted from the center of the core towards outlying sheep. Within the limitations of visual estimates, this shift away from the center of the core was proportional to the number of outlying sheep.

Variable definitions

Variables were defined as follows:

1. *Flee:* Binomial dependant variable recorded only when sheep were not travelling prior to helicopter overflights. It describes whether sheep interrupted feeding or bedding (occasionally standing inactive) to run and/or walk (often alternately) ≥10 m in response to a helicopter flying <4 km away. Its value equalled one when sheep moved ≥10 m, and equalled zero when sheep moved <10 m.
2. *Flight initiation distance:* Continuous dependant variable measuring the distance from the helicopter at which ≥1 group member(s) (almost always >50%) began to flee. It applies only to observations in which flee equalled one.
3. *Distance fled:* Continuous dependant variable describing the maximum distance (m) ≥1 group member(s) (almost always >50%) fled before ≥ 90% of the group resumed feeding or bedding. It applies only to observations in which flee equalled one.
4. *Minimum distance from trajectory:* Continuous variable measuring in km the length of the horizontal line from the sheep's pre-fleeing position to its perpendicular intersection with the projected forward trajectory of the helicopter. This variable is geometrically correlated with the horizontal component of the helicopter's angle of approach, with a smaller value implying a smaller

angle and a more direct approach (see Bulova 1994). The range of minimum distance from trajectory was 0-2.4 km (median = 0.6 km, 25% quartile = 0.3 km, 75% quartile = 1.0 km, N = 56).

5. *Relative elevation:* Continuous independent variable measuring the helicopter's elevation minus the sheep's elevation (m). The value is negative when the helicopter is below sheep. This variable is geometrically correlated with the vertical component of the helicopter's angle of approach, with a value closer to zero implying a more direct approach. Relative elevation ranged between 370 m and -270 m, but most helicopter trajectories were near the level of sheep (median = 0 m, 25% quartile = -60 m, 75% quartile = 40 m, N = 56).
6. *Distance to rocky slopes:* Continuous independent variable measuring the pre-overflight distance (m) between sheep and steep (>30°) rocky slopes. Its range was 0-1200 m. (median = 20 m, 25% quartile = 0 m, 75% quartile = 90 m, N = 56).
7. *Group size:* Continuous independent variable measuring the number of non-lambs in a group. I excluded young of the year from group size values because infant ungulates appear to recognize potential threats less readily than older conspecifics (FitzGibbon and Lazarus 1995), and their responses to risk likely are dependent on the responses of their mothers. I considered sheep to be in a group if they were on the same aspect of the same slope without cliffs or other obstructive cover blocking the line of sight between individuals (Frid 1997). Group sizes ranged from 1-64 (median = 14, 25% quartile = 6, 75% quartile = 25, N = 56).
8. *Distance to obstructive cover:* Continuous independent variable measuring the distance (km) between sheep and the nearest ridge blocking the line of sight between sheep and helicopter until the latter is past the ridge. Its range was 0.3 to 6 km (median = 2.5 km, 25% quartile = 1.5 km, 75% quartile = 3.5 km, N = 56).

Independence between observations

Multiple flights during the same day are not independent of each other, and here I present only data on the first flight of the day. Sheep were not marked. To reduce the problem of groups contributing more than 1 observation to the data set (Machlis et al. 1985), I considered observations to be independent only if they involved different groups that could be temporarily distinguished by their position in the landscape or if they occurred on different days. Because there were >200 sheep using each of the 3 study sites, and sheep groups moved constantly, merging with other groups and splintering apart, I believe that pseudoreplication was reasonably low.

Statistical analyses

I analysed fleeing probability with logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993). I built a preliminary multivariate model following procedures outlined by Hosmer and Lemeshow (1989). While readers should refer to Hosmer and Lemeshow (1989) for details, early stages of model building involved univariate tests for each independent variable. I then included in a preliminary multivariate model those variables whose univariate test statistics had probabilities of ≤0.25, and reduced the model with backwards stepping procedures. Finally, I tested for the relevant interactions (see Introduction) with a second set of backwards stepping procedures (Hosmer and Lemeshow 1989). The independent variables considered were minimum distance from trajectory, relative elevation, distance to rocky slopes, and group size.

To avoid collinearity, independent variables could not remain in the reduced model unless their condition indices were <15 (Wilkinson et al. 1996, Kleinbaum et al. 1998). Scatter plots of residuals and leverage and probability plots of residuals were used to confirm that other regression assumptions were met (Hosmer and Lemeshow 1989, Steinberg and Colla 1991). A case with an unusually low relative elevation (-460 m, the next closest value was –270 m) had extreme leverage during a preliminary model, and data were reanalysed after deleting the case. (This case is not considered by any statistics.)

Function plots of logistic regression models were generated with the equation:

$$P(\text{Fleeing}) = 1 - [(\text{EXP}(\alpha+\beta_1 X_1+\beta_i X_i))/(1+(\text{EXP}(\alpha+\beta_1 X_1+\beta_i X_i)))]$$

where α is the intercept, X_i is independent variable i, and β_i is the latter's regression coefficient (Hosmer and Lemeshow 1989, Trexler and Travis 1993).

For analyses of flight initiation distance and distance fled, I used linear regression models that were reduced to their most significant form with backwards stepping procedures (Wilkinson et al. 1996, Kleinbaum et al. 1998). This was done by first considering a preliminary model containing only main effects, and then a model containing variables that remained in the preliminary model plus their relevant second order interaction (see Introduction). Variables considered were the same as for analysis of fleeing probability, except that distance to obstructive cover was considered also for analysis of flight initiation distance. Log transformations (base 10) and standard diagnostic tests (condition indices, plots of residuals and leverage) were used to ensure that regression assumptions were met (Zar 1984. Wilkinson et al. 1996, Kleinbaum et al. 1998).

Other statistical tests used are common-place and described in Zar (1984). Analyses were done using SYSTAT 8.0 (SPSS 1998). This program, however, does not provide diagnostics nor confidence limits for logistic regression coefficients, which I obtained with LOGIT 2.0 (Steinberg and Colla 1991) and JMP (SAS Institute Inc. 1996), respectively.

RESULTS

Sheep groups fled during overflights in 43 of 56 observations (77%). During 13 observations (23%), all sheep in a group did not respond overtly or only became vigilant. Animals ran (sometimes combined with walking) in 37 of 43 fleeing events (86%), and walked during remaining events. In general, sheep first stared at the helicopter and then alternated movement with vigilance bouts.

Most group members escaped in relative synchrony. The initial run or walk away from the helicopter included >50% or 100% of the group, respectively, during 62% and 48% of fleeing events (N = 42 [one observation had missing data]). Even when sheep delayed flight relative to other group members, all sheep fled in 76% of fleeing events (N = 42, one case had missing data).

To flee or not flee

According to the reduced logistic regression model (Table 1; $Rho^2 = 0.66$), the probability of sheep fleeing depended on the multiplicative effect of minimum distance from trajectory and distance to rocky slopes. (A preliminary model considering only the additive effects of these factors, explained 5 % less of the variability in the data and had coefficients with larger standard errors than the model with the interaction.) Fleeing probability decreased as minimum distance from trajectory increased, but did so at a higher rate when sheep were on rocky slopes than when sheep were 5-20 m from rocky slopes. Furthermore, sheep farther than 20 m of rocky slopes always fled, regardless of minimum distance from trajectory (within a 2.0 km range) (Fig. 1; Table 1). Although admittedly there were few observations for non-fleeing sheep that were 5-20 m from rock slopes, a descriptive plot corroborated the trends estimated by the logistic regression model (Fig. 2).

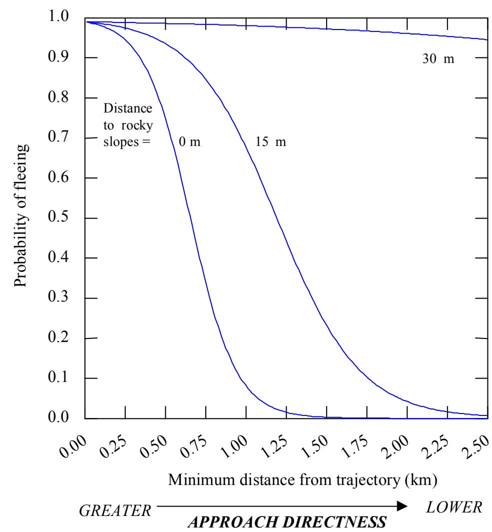

Fig. 1. Estimated fleeing probabilities as a function of the interaction between minimum distance from trajectory and distance to rocky slopes. Curves were generated with parameters of the reduced logistic regression model of Table 1 ($Rho^2 = 0.66$).

Table 1. Reduced logistic regression model estimating fleeing probability

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	*P*
Intercept	4.61	2.10	9.26	2.63	0.009
minimum distance from trajectory * distance to rocky slopes	0.21	0.09	0.42	2.70	0.007
minimum distance from trajectory	-7.04	-14.10	-3.41	-2.74	0.006

Log likelihood =-30.34, Chi-squared = 40.05, DF = 2, N = 56, $P<0.001$, $Rho^2 = 0.66$, N = 43 groups that fled, 13 that did not flee.

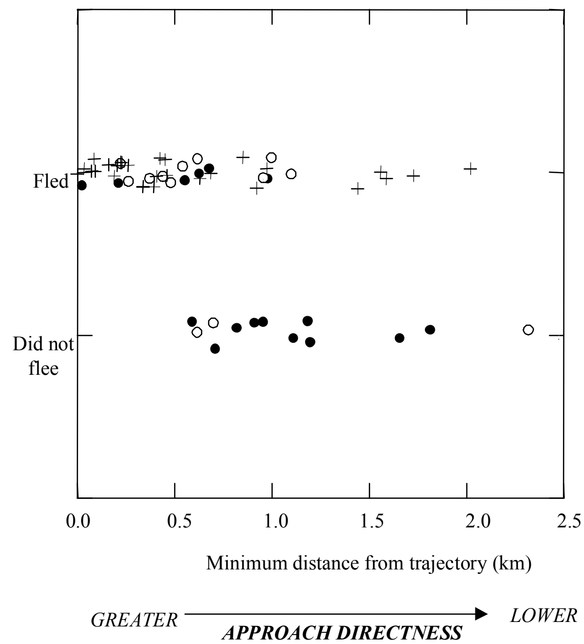

Fig. 2. Scatterplot of flee vs. no flee responses, as affected by the interaction between minimum distance from trajectory and distance to refuge. Dark circles represent sheep on rocky slopes, open circles represent sheep 5-20 m from rocky slopes (median = 20 m), crosses represent sheep 25-1200 m from rocky slopes (median = 100 m). Points are jittered so that overlapping data can be read. Figure is descriptive only because distance to rocky slopes was analysed as a continuous variable in the logistic regression (see Table 1, Fig. 1).

Group size was excluded from the reduced model, possibly because of limited statistical power. A univariate model of fleeing probability fitted during the first stage of model building, however, suggested that larger groups were more likely to flee than smaller groups (-log likelihood ratio = 30.34; Chi square = 5.87; P = 0.016; Rho^2 = 0.10).

I found no significant effect of the helicopter's relative elevation. This variable did not enter the preliminary multivariate model (Univariate Wald test during early model building stage [Hosmer and Lemeshow 1989]: t = 1.055, DF =1, P = 0.29). Descriptive plots indicated that the lack of effect was not because of an inverse U-shaped function (i.e., sheep not fleeing at very high and very low relative elevations, but fleeing at intermediate elevations), which would not be detected by a logit assuming linearity (Hosmer and Lemeshow 1989).

Pooling the sexes for analyses appeared to be justified. When I tested the reduced model using only data on female-young groups, coefficients changed little and the overall model was significant (Log-likelihood ratio = -21.59, Chi-square = 31.33, DF = 2, P <0.001, N = 27 groups that fled, 10 groups that did not flee; 1 case with large leverage was excluded from analyses). Wald tests for independent variables, however, were marginally not significant (P = 0.067, 0.072) because of the reduced sample size and power.

Flight initiation distance

Flight initiation distance ranged from 100 m to 3 km, and had a median value of 0.9 km (25% quartile = 0.5 km, 75 % quartile = 1.5 km, N = 42 [one observation had missing data]). According to the reduced linear regression model (Table 2; R^2 = 0.59), flight initiation distance increased as minimum distance from trajectory became greater and decreased as relative elevation increased (Fig. 3). Flight initiation distance also increased as group size and distance to obstructive cover became greater (Fig. 4).

Distance fled

Distance fled ranged from 15 m to 1.5 km, and had a median value of 100 m (25% quartile = 30 m, 75% quartile = 200 m, N = 43). Sheep tended to run towards rocky slopes and, according to the reduced regression model (F = 4.40, DF = 1,41, P = 0.042), distance fled increased as distance to rocky slopes became greater (Fig. 5). The relationship, however, was weak (R^2 = 0.10) because sheep on rocky slopes fled during very direct approaches, and because sheep that were not on rocky slopes prior to overflights often kept fleeing after reaching these slopes (Fig. 5).

Fleeing responses in relation to weeks of cumulative overflights

This analyses is limited to observations made at Hoge Pass, which was the only site were I collected data over several weeks. There was 25-day gap in observations between Week 1 (26 June-1 July) and Weeks 2-3 (respectively, 25-31 July and 2-8 August).

The proportion of sheep fleeing was lowest during the first week of overflights but there was no difference between the second and third week (Fig. 6, Yates corrected Chi-square = 7.18, DF = 2, *P* = 0.03). This observation was not confounded by minimum distance from trajectory nor distance to rocky slopes (Fig. 6), which on average did not differ between weeks of observation (ANOVA on log-transformed data for minimum distance from trajectory: F = 1.22, DF = 2,46, *P* = 0.30; for distance to rocky slopes: F = 0.18, DF = 2,46, *P* = 0.84).

Table 2. Reduced linear regression model estimating flight initiation distance.

Variable	Regression coefficient ± standard error	Standardized coefficient	Condition index	t-value	P
Intercept	0.0 ± 0.056			0.003	1
group size	0.10 ± 0.042	0.2.8	1.94	2.37	0.02
minimum trajectory dist.	0.52 ± 0.12	0.48	4.18	4.25	<0.001
dist. to obstructive cover	0.032 ± 0.01	0.37	4.45	3.33	0.002
relative elevation	-0.024 ± 0.009	-0.31	10.26	-2.68	0.01

F = 13.51; DF = 4,37, P<0.001, R^2 = 0.59. Variables were log transformed except for distance to obstructive cover.

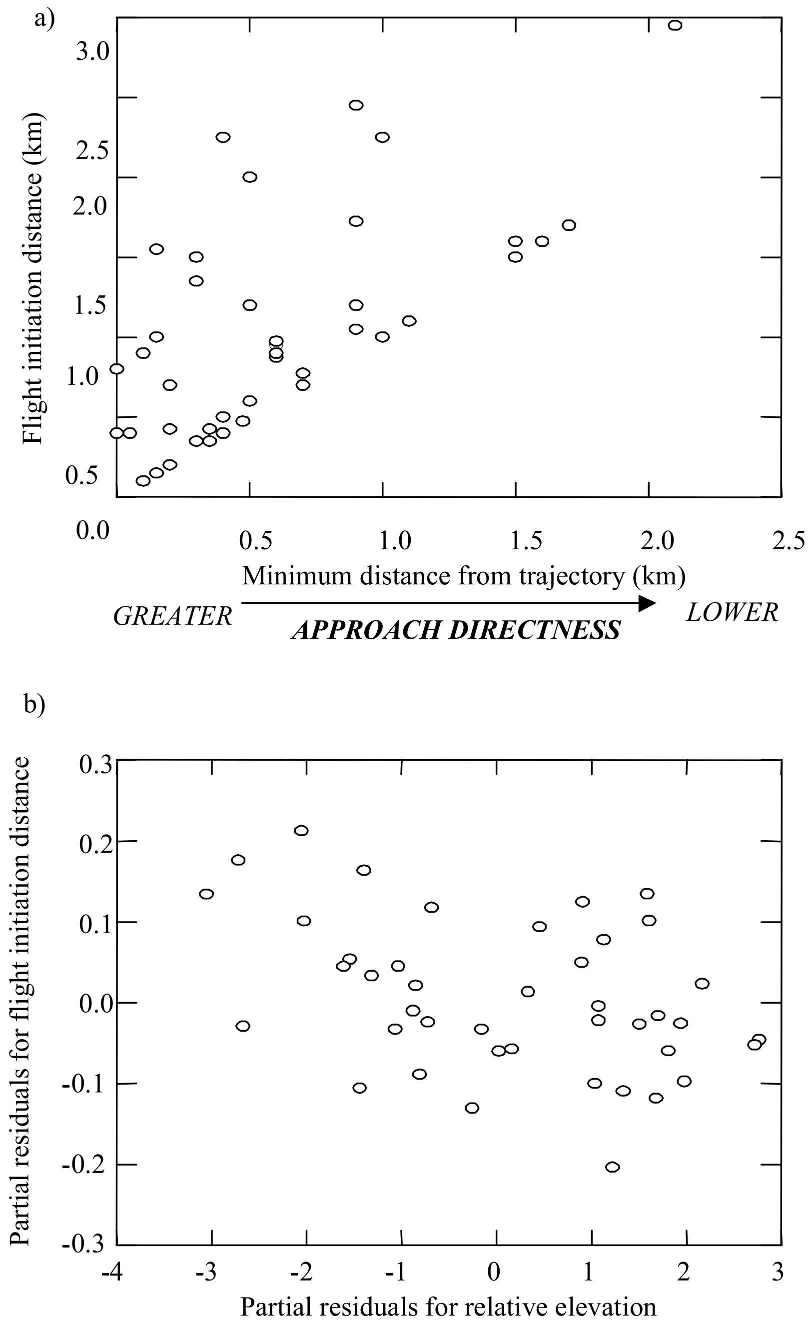

Fig. 3. Relationship between flight initiation distance and (a) minimum distance from trajectory and (b) relative elevation. The scatterplot involving minimum distance from trajectory is only descriptive because it does not account for the effects of group size, relative elevation and distance to obstructive cover. The scatterplot for relative elevation is based on partial residuals because the effect was not strong enough to be shown without adjusting for the effect of other variables (see Wilkinson et al. 1996).

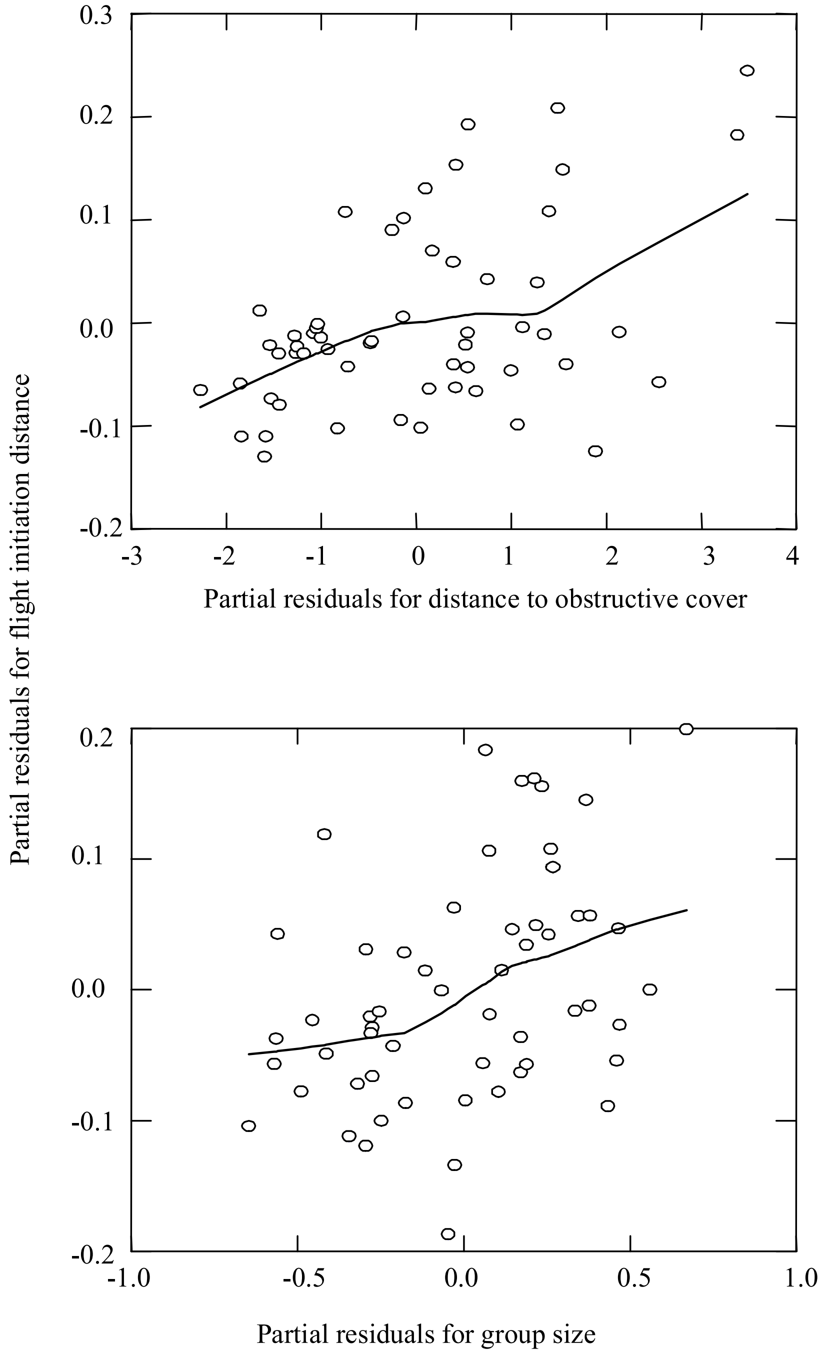

Fig. 4. Plots of partial residuals illustrating the effects of (a) distance to obstructive cover, and (b) group size on flight initiation distance. Partial residuals were used instead of actual data because trends were not strong enough to be shown without controlling for the influence of other factors affecting flight initiation distance (see Table 2). Trend lines are drawn with LOWESS smoothing at tension = 0.8 (Wilkinson et al. 1996), and are descriptive only. See Table 2 for the reduced regression model.

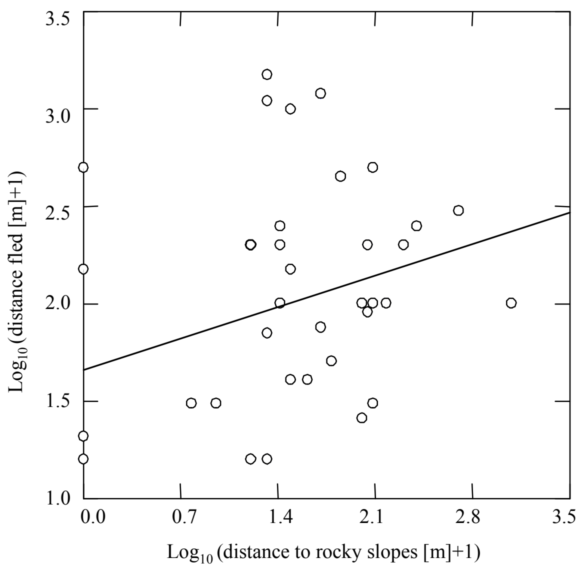

Fig. 5. Distance fled in relation to distance from rocky slopes (y = 1.66 + 0.23x, R^2 = 0.10).

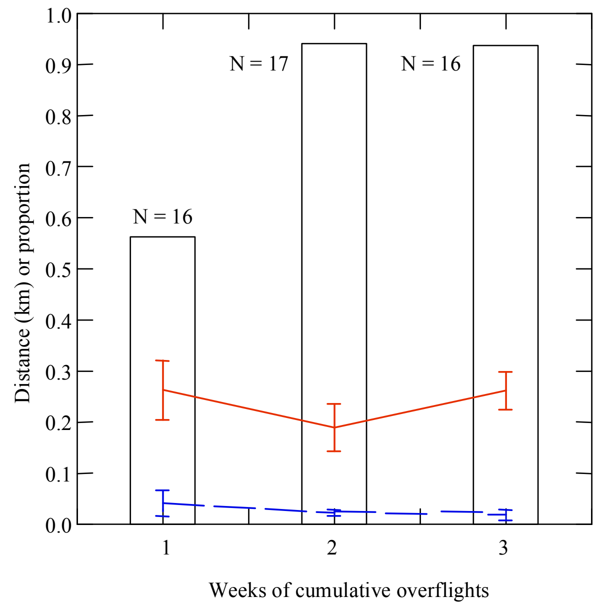

Fig. 6. Proportion of sheep groups fleeing (bars) in relation to weeks of cumulative overflights at Hoge Pass. Solid line is the weekly mean of minimum distance from trajectory, and broken line is the weekly mean of distance to rocky slopes. Error bars are standard errors of the mean.

DISCUSSION

Results generally were consistent with the hypothesis that sheep would treat the decision to flee from helicopters as a trade-off between energetics and predation risk (see Ydenberg and Dill 1986). They also confirm that while these trade-offs are important, flight initiation distance is partially a function of perceptual constraints (Burger and Gochfeld 1981, Ydenberg and Dill 1986, Dill and Ydenberg 1987).

Data supported the predictions that the probability of sheep fleeing would be inversely related to the helicopter's angle of approach (as indexed by minimum distance from trajectory) and directly related to distance from rocky slopes. The effect of these 2 factors, however, was multiplicative. Fleeing probability decreased at a faster rate for sheep on rocky slopes than for sheep 5-20 m from these slopes, and sheep >20 m from rocky slopes always fled, even if the helicopter approached very indirectly. (These relationships were not an artifact of my definition of fleeing - sheep moving ≥10 m - because rocky slopes did not create a boundary limiting how far sheep fled; see Results for distance fled.) The main effect of approach directness is consistent with observations of mountain goats (*Oreamnos americanus*) exposed to helicopter overflights (Côté 1996), and with tests of economic models of prey fleeing from predators (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998). I detected an effect of angle of approach only in a 2-dimensional plane probably because sample sizes of very low and very high relative elevations were insufficient to test for the vertical component of approach directness. The main effect of distance from rocky slopes is consistent with economic models of prey fleeing from predators in which prey near a refuge have a lower "cost of remaining" (i.e., they are more likely to reach the refuge before the predator reaches them), and thus may avoid energetic costs of fleeing that do not contribute substantially to safety (Ydenberg and Dill 1986). Admittedly, it is unclear why rocky slopes affect responses by adult sheep to a simulated aerial predator (i.e., helicopter). Rocky slopes are a refuge for adult sheep from cursorial predators, such as wolves (*Canis lupus*) and coyotes (*C. latrans*) (Berger 1991; review in Frid 1997), and only lambs are preyed on by aerial predators such as golden eagles (*Aquila chrysaetos*: Nette et al. 1986). While distance to rocky slopes affected fleeing probability, it did not affect flight initiation distance. Group size was excluded from the multivariate model of fleeing probability possibly because of limited statistical power; larger sample sizes are needed to investigate its effect.

My observation that distance to rocky slopes and approach directness had a multiplicative effect on fleeing is consistent also with prior studies which found that the antipredator responses by prey exposed to a given risk factor may depend on the level of risk created by other factors. For example, Kramer and Bonenfant's (1997) woodchuck (*Marmota monax*) study, found that the relationship between distance to refuge and flight initiation distance was steeper when a person simulating a predator approached, relative to the woodchuck's position, from the opposite side of a refuge (and thus the woodchuck had to run towards the person to reach the refuge) than when the person approached from the same side of the refuge. Other examples can be found in Burger and Gochfeld (1981, 1990) and Cooper (1997, 1998). Multiplicative effects may be important not only for fleeing decisions, but also for other types of antipredator behavior. For example, I found that individual vigilance decreased as group size became greater in Dall's sheep, but did so at lower rates as distance to rocky slopes decreased (Frid 1997). Antipredator behavior may not always depend on multiplicative effects, however, as was the case for flight initiation distance and distance fled in my study. Further theoretical work is needed to predict a priori when multiplicative effects should be expected.

In contrast to my prediction and the results of other studies (Burger and Gochfeld 1980, 1991; but see Bulova 1994), flight initiation distance increased as the horizontal component of approach directness decreased. While the mechanisms are unclear, this observation likely is related to the geometric correlation between approach directness and minimum distance from trajectory and, as Fig. 3 indicates, to most sheep fleeing when the helicopter reached its nearest horizontal distance to them (i.e., when the point in the trajectory was at 90 degrees from the sheep's position).

Flight initiation distance increased with group size, suggesting that the effect of more sensory organs was stronger than the risk-dilution effect (Ydenberg and Dill 1986, Dill and Ydenberg 1987). In other words, results suggest that as group size increases the probability that a given individual will see a far away helicopter and begin to flee becomes greater, and sheep unaware of the helicopter flee because of cues taken from conspecifics. Flight initiation distance increased also with distance to obstructive cover, which is consistent with findings of other studies suggesting that flight initiation distance is affected by perceptual constraints (Burger and Gochfeld 1981; review in Ydenberg and Dill 1986).

As predicted, sheep tended to flee towards rocky slopes, and distance fled increased as distance to rocky slopes became greater. Although the relationship was weak, largely because sheep kept fleeing after reaching rocky slopes, it is consistent with the expectation that fleeing should be done such that it decreases risk of capture (Ydenberg and Dill 1986). The decision to flee towards rocky slopes, however, may be confounded by the aircraft almost always approaching from a gap in mountainous topography and from the direction opposite from rocky slopes; thus, I cannot disprove the possibility that sheep were merely fleeing away from aircraft and rocky slopes happened to be in that direction. It is interesting that while approach directness strongly affected fleeing probability, it did not affect distance fled. This results rejects my prediction and contrasts with prior research (Bulova 1994).

I did not find evidence of habituation. At Hoge Pass sheep fled during each week of cumulative observation, with the lowest proportion (63%) occurring during the first week. While data did not support the hypothesis that animals should habituate to non-lethal human disturbance, thus avoiding unnecessary investments in antipredator behavior (Burger and Gochfeld 1981, 1990), my study may have been too short for a proper test. Multi-year research on helicopter disturbance, however, concluded also that bighorn sheep (*O. canadensis*) did not habituate substantially to overflights (Bleich et al. 1994).

Conservation implications

Ungulate populations may be highly variable in size due to predation (Ross et al. 1997) and forage availability (Caughley and Gunn 1993). Thus, rigorous quantification of the effects of helicopter disturbance on population dynamics requires multi-year studies of radio-collared individuals exposed to experimentally determined disturbance rates. Such expensive projects rarely will be an option, and my study was no exception.

Experimental studies of the consequences of disturbance on ungulate fitness are limited to mule deer (*Odocoileus hemionus*) disturbed by an all-terrain vehicle (Yarmoloy et al. 1988), and caribou (*Rangifer tarandus*) disturbed by low elevation jet flights (Harrington and Veitch 1992). These studies found that individual fitness decreased with increased disturbance rates (Yarmoloy et al. 1988, Harrington and Veitch 1992), but are based on few study animals and the generality of results is controversial. Nonetheless, their results are consistent with theoretical models of caribou disturbed by seismic exploration (Bradshaw 1994) and military jet overflights (Luick et al. 1996), and with correlational evidence of a caribou population decreasing as rates of military jet overflights increased (Maier 1996).

As suggested by the above studies, whether fleeing responses and other disruptions of activity budgets caused by helicopter disturbance actually affect the body condition and, consequently, reproductive success, of Dall's sheep, likely depends on the rate of overflights. The potential impact is a legitimate concern, as sheep exposed to long-term helicopter disturbance have not been found to habituate substantially (Bleich et al. 1994).

Results provide a first step towards predicting and, if necessary, mitigating the fitness and population consequences of helicopter disturbance on Dall's sheep. The current application of my results, however, is limited because (1) they are based on one population during one season, (2) do not necessarily address all of the relevant factors affecting fleeing decisions, and (3) do not provide evidence that disturbance actually affects fitness. However, the results do provide preliminary parameters for models predicting energetic costs incurred as a function of fleeing rate, distance fled, and time lost from rumination and foraging. Such models could determine which disturbance rates sheep can incur without suffering fitness costs. Once this prediction is made for a given population, logistic regression models of fleeing probability, similar to the one I present here, could be used to predict the minimum distances from trajectory that would result in an acceptably low disturbance rate. (Wildlife managers using my logistic regression model should heed confidence intervals [Table 1]). While angle of approach is the biologically relevant variable affecting fleeing probability, minimum distance from trajectory is geometrically correlated to the horizontal component of this angle, is controllable by pilots, and thus would be the focus of pilot guidelines to reduce disturbance of sheep. Models of fleeing probability could also account for seasonal and/or diurnal variability in the sheep's distance to rocky slopes (see Fig. 1), and pilot guidelines could be adjusted accordingly. While my study was not designed to explicitly test for effects of the vertical component of approach directness—the helicopter's relative elevation—future work should address whether horizontal setback distances for pilots can be relaxed when helicopters are very high above or very far below sheep ranges.

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BEHAVIORAL RESPONSES BY DALL'S SHEEP TO OVERFLIGHTS BY FIXED-WING AIRCRAFT

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Abstract: Are behavioural responses by Dall's sheep (*Ovis dalli dalli*) exposed to overflights by a light fixed-wing aircraft consistent with economic models of antipredator behaviour? Agreeing with such models, the probability of active sheep fleeing and of bedded sheep un-bedding increased as aircraft approached more directly. Un-bedding probability was affected by the vertical and horizontal components of angle of approach, as indexed by the sheep's minimum distance from the aircraft's trajectory and relative elevation, respectively. Fleeing probability was affected only by the horizontal angle of approach, possibly because trials in which the aircraft was very high above sheep were few. When active sheep fled during overflights, the time they neither fed nor bedded increased as angle of approach decreased. Active sheep did not feed less or move more within 10 min after overflights than prior to disturbance. Almost all bedded sheep that interrupted resting bouts, however, were active for 44-100% of the post-overflight period, suggesting that the energetic costs of interrupting rumination were greater than those of decreased foraging and increased locomotion. Sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and do not warrant costly antipredator responses, but there was no evidence of habituation. This study provides parameters for models predicting energetic and fitness costs incurred as a function of overflight rates, and logistic regression models of fleeing and un-bedding probability that could be used to create pilot guidelines to mitigate disturbance. Results support that fixed-wing aircraft are substantially less disturbing to sheep than helicopters.

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Human disturbance may create energetic costs to animals by displacing them from feeding sites, decreasing foraging time, interrupting resting bouts, and increasing movement (e.g. Stockwell et al. 1991; Côté 1996; Sutherland 1996; Gill et al. 1996; Maier et al. 1998; White et al. 1999). Theoretical models predict that if these costs occur at a high rate, disturbance could jeopardize the body condition, reproductive success (Bradshaw 1994, Gill et al. 1994, Luick et al. 1996, White et al. 1999) and population dynamics of wildlife (Gill et al. 1994, Sutherland 1996).

It is difficult to quantify empirically the reproductive consequences of motorized disturbance on ungulates. The few experimental studies that have attempted the task found that fitness decreased as disturbance rates increased (Yarmoloy et al. 1988, Harrington and Veitch 1992), which is consistent with theoretical predictions (e.g. Bradshaw 1994, Luick et al. 1996). These experimental studies, however, had small sample sizes and the generality of their conclusions is controversial. Correlational studies suggest that high rates of motorized disturbance could cause ungulate populations to decline (Joslin 1986, Maier

1996), but their study designs lacked the replicated control sites that could rigorously test disturbance effects (Underwood 1994). Thus, empirical studies have yet to make strong inferences on the functional relationship between motorized disturbance and the fitness and population dynamics of ungulates. Collectively, however, prior work does suggest that the potential effect of motorized disturbance on wildlife deserves further consideration. Concern for potential effects may be particularly relevant for mountain sheep (*Ovis* sp.), which habituate only partially to strong stimuli, such as helicopter overflights (Bleich et al. 1994).

A comparison of prior studies suggests that mountain sheep respond more strongly to helicopter overflights (Stockwell et al. 1991, Bleich et al. 1994, Frid 1999*a*) than to fixed-wing aircraft (Krausman and Hervert 1983, Bleich et al. 1994) and military jet overflights (Krausman et al. 1998). Fixed-wing aircraft, however, still may disturb sheep substantially. Krausman and Hervert (1983) found that sheep moved >100 m during 19% of observations when the plane flew directly towards sheep and circled them up to 10 times.

In this study I analyze responses by Dall's sheep (*O. dalli dalli*) to overflights by a light fixed-wing aircraft and relate results to sheep conservation. My framework is based on economic models of antipredator behavior predicting that prey should maximize fitness by making optimal decisions that consider the trade-off between energetics and safety (e.g. Ydenberg and Dill 1986, Lima and Dill 1990, Bulova 1994). It is based also on the hypothesis that animals respond similarly to human disturbance and predation risk (Gill et al. 1996, Sutherland 1996). To my knowledge, no other work on disturbance by fixed-wing aircraft has focused on Dall's sheep or considered most of the variables I analyzed.

My first prediction was that the probability of active sheep fleeing and of bedded sheep interrupting a resting bout would decrease as the minimum distance between sheep and the plane's trajectory increased, and as the plane's elevation relative to sheep became greater. The basis for this prediction is that minimum distance from the trajectory and relative elevation are geometrically correlated to the plane's three-dimensional angle of approach, with a shorter distance and lower relative elevation implying a smaller angle and a more direct approach (see Bulova 1994). Direct approaches might indicate that the predator has detected the prey and intends to capture it (reviews in Cooper 1997, 1998). Not surprisingly, prior studies found that the proportion of prey fleeing and their distance from the predator at which they began to flee increased when predators (as simulated by humans) approached more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998; see Bulova 1994 for an exception). Studies of mountain Caprinae disturbed by aircraft also provide a basis for this prediction; animals were less likely to flee as minimum distance from trajectory (Côté 1996; Frid 1999*a*) or as the aircraft's relative elevation became greater (Krausman and Hervert 1983). As an extension of this prediction, I expected that the time that sheep interrupted feeding or bedding would be inversely related to the plane's angle of approach (see Côté 1996).

My second prediction was that sheep farther from rocky slopes would be more likely to flee or interrupt resting bouts than sheep near or on rocky slopes. The basis for this prediction is that rocky slopes are a refuge from cursorial predators for sheep (review in Frid 1997), and sheep may be more responsive to any threatening stimuli while far from refuge (see Ydenberg and Dill 1986, Dill and Houtman 1989, Bulova 1994, Kramer and Bonenfant 1997). While it is unclear how the sheep's perception of risk from a simulated aerial predator (i.e. aircraft) relates to mountainous terrain (only lambs are preyed on by aerial predators, such as golden eagles (*Aquila chrysaetos*: Nette et al., 1986), the prediction is based also on observations of sheep farther from rocky slopes being much more likely to flee during helicopter overflights (Frid 1999*a*). Unfortunately, while collecting data for analyses presented here, sheep almost always were on or near rocky slopes, which contrasted sharply with my prior observations (Frid 1997, 1999*a*). Thus, the prediction was rejected while I was still in the field, and distance to rocky slopes was analyzed only as a statistical control.

Thirdly, I predicted that time spent foraging would be lower and time spent moving would be greater after than before overflights, and that bedded-sheep that interrupted resting bouts would spend less time bedded after overflights. The basis for this prediction is that after a predator encounter, prey may remain alert and not resume energy-gaining activities for some time after the predator is no longer visible, but potentially could return (review in Lima and Dill 1990). This prediction is based also on observations of mountain sheep foraging less efficiently, increasing movement, or spending less time bedded after helicopter overflights (Stockwell et al. 1991, Bleich et al. 1994, Frid 1999*b*).

Finally, I predicted that sheep would become more tolerant of direct approaches by the plane as cumulative weeks of overflights increased. Predicting habituation is within the framework of economic models of predator avoidance because sheep would increase fitness if they learn that aircraft overflights are not a lethal threat and therefore do not warrant the energetic costs of antipredator behaviour (see Burger and Gochfeld 1981, 1990).

METHODS

Study site and season

I collected data between 22 June and 15 July 1999, at Hoge Pass (ca. 61 °19' N, 139° 33' W), Kluane National Park Reserve, southwest Yukon Territory, Canada. The site is roadless and rugged. It consists of alpine habitats without shrubs or tree cover. Large meadows are found at the base of steep, rocky terrain and sheep predators (including grizzly bears [*Ursus arctos*] and wolves [*Canis lupus*]) are common. At least 200 sheep used the study area.

Hoge Pass is the same site where I studied helicopter disturbance of sheep during 1997 (Frid 1999*a*, 1999*b*). Fixed-wing and helicopter traffic occurs mainly between May and September, perhaps averaging 25 flights per season for each aircraft type (not including flights related to my studies), but precise records are lacking. The study area was overflown multiple times per day by commercial jet planes travelling at very high elevations (several thousand meters above); it is plausible that such traffic may have made sheep less sensitive to experimental overflights that were far from sheep and/or high above them.

Animals sampled

Data presented are for adult females (two years or older). I intended to reduce potential sources of variability by sampling only females with young. Perhaps due to the cold wet spring that preceded fieldwork, however, there was a large proportion of barren females and sampling mothers only would have resulted in small sample sizes. Thus, 41% of 81 observations analyzed for immediate responses were of females without young. Preliminary analyses found no effect of reproductive status on responses to aircraft (contingency table analyses for proportion of active sheep fleeing: Pearson Chi-square = 0.072, DF = 1, N = 51, P = 0.79; for proportion of bedded sheep un-bedding: Yates-corrected Chi-square = 0.001, DF = 1, N = 30, $P = 0.98$), and reproductive status is not considered further.

Sheep were not marked. To reduce the problem of individuals contributing more than one observation to the data set (Machlis et al. 1985), I considered observations to be independent only if they involved individuals from different groups during the same overflight. Sheep groups using the same area for several days were sometimes sampled during more than one overflight. I believe, however, that pseudoreplication of focal individuals was quite low because there were >200 sheep using the area and groups moved constantly, merging with other groups and splintering apart.

Experimental overflights

Sheep were exposed to 42 overflights by a single fixed-wing aircraft (Cessna 206). Analyses, however, include only 32 overflights because the GPS system failed to record trajectories during six overflights (see below), and because all focal animals were strongly affected by the plane circling during four overflights. The plane was stationed outside the study area and was called in via satellite phone to overfly sheep following an explicit trajectory. Depending on weather, there were 0-3 overflights per day, with ≥8 hours between overflights. (Poor visibility precluded overflights during four days.) Sheep were disturbed by two helicopter overflights related to camp logistics at the onset of the study, plus helicopter activity unrelated to our work during two days. Sheep were not sampled for ≥8 hours after a helicopter flew through the area.

Analyses consider only overflight trajectories in which the plane followed a straight path through the study area and did not circle over focal individuals. (Exceptions were two cases in which the plane circled after the initial response by sheep, for which only fleeing probability was analyzed, and two cases in which the plane circled in line of sight of bedded sheep that did not un-bed.) Within the restrictions of pilot safety, weather, and topography, I reduced uncontrolled variability by designing trajectories that met the following criteria:

1. No substantial turns or changes in relative elevation within 3 km of the focal animal (see Cooper 1998). Two cases were excluded from analyses because the aircraft turned directly towards sheep within 1.5 km of them.
2. No topographic features that could block the line of sight between sheep and plane within 2 km of focal sheep (see Frid 1999*a*). One case was excluded from analyses because this requirement was not met.
3. Consistent aircraft speed (see Ydenberg and Dill 1986). Mean ± SD ground speed was 197 ± 16 km/h (N = 38 overflights).

I defined overflights as the time the plane was within 4 km of sheep while approaching and exiting the area. This 4-km threshold is based on the 75% quartile of the distance between animals and aircraft at which active sheep became vigilant towards the plane (3.8 km, N = 38 focal sheep). I divided time relative to overflights into three experimental periods:

1. *Pre-overflight*: 10 min prior to overflights.
2. *During overflight*: the time when the plane was ≤4 km of sheep, which had a mean ± *sd* duration of 128 ± 23 seconds (range 55-186 s, N = 48 focal animal for which post-overflight behaviour was recorded).
3. *Post-overflight*: 10 min after overflights.

Recording behaviour and other sheep-related data

Two assistants and I observed focal individuals from the ground, from distances of >1 km and using spotting scopes. Only one focal individual per group was observed during a given overflight. Unless <3 groups were observable, we made three observation per overflight (1/observer). We obtained continuous behavioural records of focal individuals (Martin and Bateson 1993) using either a notebook computer programmed as an event recorder (ca. 1/3 of samples), or by speaking observations into tape recorders. In the latter case, tapes were transcribed into electronic files with the event recorder.

Focal animal samples began ≥10 min prior to overflights and continued for ≥10 min after the plane left the study area. Samples were shorter, however, if the plane arrived earlier than expected or if sheep went out of sight behind topography. Variability in sample duration may affect variability in the proportions of time focal animals spent on different behaviors during the sample (Frid unpublished data). Thus, for the pre- and post-overflight periods I reduced longer samples to 10 min, and excluded samples that were <9 min from analyses of behaviour in relation to experimental stage.

Recording aircraft trajectories and sheep locations

The pilot recorded aircraft trajectories with a Trimble Geo Explorer II GPS system, which was programmed to record one location per second. Trajectories recorded in the field were later corrected with data from a base station. Sheep locations were plotted shortly before beginning focal animal samples using compass bearings and 1:50,000 topographic maps.

After fieldwork, locations of focal sheep were transcribed into the GIS files containing the corresponding overflight trajectory. Variables involving the sheep's location and/or timing of sheep behaviour in relation to the plane's position (see below) were measured using Pathfinder Office V.2 (Trimble Navigation Limited 1996). Because sheep locations were less precise than trajectory records (partly because active sheep may have moved during the pre-overflight period), values of horizontal spatial variables were rounded-off to the nearest tenth of a kilometer.

Variable definitions

I will refer to focal animals that were active and bedded when overflights began, respectively, as *active sheep* and *bedded sheep*. Variables requiring definitions and which represent responses to the approaching plane are as follows:

1. *Flee*: Binomial variable quantifying the proportion of active sheep that ran and/or walked ≥10 steps before stopping for ≥10 s to be vigilant or feed, vs. the proportion that moved 0-9 steps.
2. *Un-bed*: Binomial variable quantifying the proportion of bedded sheep that stood up to be vigilant and/or flee, vs. the proportion that remained bedded.
3. *Vigilance initiation distance*: Continuous variable measuring in km the distance from aircraft at which active sheep became vigilant towards the plane.
4. *Time not foraging or bedded*: Continuous variable that applies to active or bedded sheep that fled or un-bedded. It measures in seconds the time between the first overt response towards aircraft and when the focal animal bedded or began to feed continuously for ≥5 s, without interrupting either activity by walking and/or being vigilant for >1 min.

Independent variables are defined below. (Note that distributions of independent variables reported for bedded sheep do not include cases excluded from analyses, as described under Data Analyses.)

1. *Minimum distance from trajectory*: Continuous variable measuring in km the length of the line from the sheep's pre-fleeing position to its perpendicular intersection with the projected forward trajectory of the plane. This variable is geometrically correlated with the plane's angle of approach, with a smaller value implying a smaller angle and a more direct approach (Bulova 1994). The range of minimum distance to trajectory was 0-3.7 km for active sheep (median = 0.3 km, 25% quartile = 0.2 km, 75% quartile =0.8 km, N = 51 focal animal samples), and 0-2.9 km for bedded sheep (median = 0.4 km, 25% quartile = 0.1 km, 75% quartile =0.7 km, N = 30).
2. *Relative elevation*: Continuous independent variable measuring the plane's elevation minus the sheep's elevation (m). Values are negative when the plane was below sheep. Relative elevation ranged between -210 m and 560 m for active sheep (median = 30 m, 25% quartile = -30 m, 75% quartile = 140 m, N = 51 focal animal samples), and from -60 m to 380 m for bedded sheep (median = 80 m, 25% quartile = 30 m, 75% quartile =190 m, N = 30).
3. *Distance to rocky slopes*: Continuous independent variable measuring the pre-overflight distance (m) between focal sheep and steep (>30°) outcrops or scree slopes. Its range was 0-750 m for active sheep (median = 5 m, 25% quartile = 0 m, 75% quartile =15 m, N = 51 focal animal samples) and 0-100 m for bedded sheep (median = 0 m, 25% quartile = 0 m, 75% quartile = 3 m, N = 30 focal animal samples).

Data analyses

I analyzed fleeing and un-bedding probabilities with logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993). I built preliminary multivariate models following procedures outlined by Hosmer and Lemeshow (1989), and then reduced these models to their most significant form with backwards stepping procedures. While readers should refer to Hosmer and Lemeshow (1989) for details, early stages of model building involved univariate tests for each independent variable. I then included in a preliminary multivariate model those variables whose univariate test statistics had probabilities of ≤0.25, and reduced the model with backwards stepping procedures. If the reduced model was multivariate, I then tested for interactions with a second set of backwards stepping procedures (Hosmer and Lemeshow 1989). The independent variables considered were minimum distance from trajectory, relative elevation, and distance to rocky slopes.

I expected the effect of relative elevation to be an inverse U-shape function, with animals not responding at very low and very high elevations. Sample sizes, however, were marginal for following procedures necessary to detect a non-linear logit (Hosmer and Lemeshow, 1989). Thus, un-bedding probability was analyzed after eliminating the inverse U-shape effect by excluding three cases with relative elevations of <-60 m. (The three cases were excluded from all other analyses as well). Preliminary analyses for the inverse U-shape function (Hosmer and Lemeshow 1989) did not detect an effect of relative elevation on fleeing probability, and thus no cases with low relative elevations were deleted for analyses of this variable (see Results).

If the reduced model was multivariate, I assessed collinearity with condition indices (Wilkinson et al., 1996; Kleinbaum et al., 1998). These were derived from eigenvalues calculated with factor analyses. Independent variables could not remain in the reduced model unless their condition indices were <15 (Wilkinson et al. 1996). Scatter plots of residuals and leverage and probability plots of residuals were used to confirm that other regression assumptions were met (Hosmer and Lemeshow 1989; Steinberg and Colla 1991). For the un-bed probability model, a case with an unusually large distance to rocky slopes had extreme leverage during a preliminary model, and data were reanalyzed after deleting the case.

Function plots of logistic regression models were generated with the equation:

$$P(Y) = 1- [(EXP(\alpha+\beta_1 X_1+\beta_i X_i))/(1+(EXP(\alpha+\beta_1 X_1+\beta_i X_i)))]$$

where P (Y) is either the probability of fleeing or un-bedding, α is the intercept, X_i is independent variable i, and β_i is the latter's regression coefficient (Hosmer and Lemeshow 1989, Trexler and Travis 1993).

Time not foraging or bedded was analyzed with separate linear regression models for active and bedded sheep. The model for active sheep considered the same variables as for the logistic regression models and was reduced to its most significant form with backwards stepping procedures (Wilkinson et al. 1996, Kleinbaum et al. 1998). For bedded sheep, small sample sizes allowed the model to consider only one variable, which I chose to be minimum distance from trajectory. Log transformations (base 10) and standard diagnostic tests (plots of residuals and leverage) were used to ensure that regression assumptions were met (Zar 1984, Wilkinson et al. 1996, Kleinbaum et al. 1998). An outlier with high values for the dependent variable and for minimum distance from trajectory had large leverage during a preliminary model for active sheep, and data were reanalyzed after deleting the case.

Other statistical tests used are commonplace and described in Zar (1984). Analyses were done using SYSTAT 8.0 (SPSS 1998). This program, however, provides neither diagnostics nor confidence limits for logistic regression coefficients, which I obtained with LOGIT 2.0 (Steinberg and Colla 1991) and JMP (SAS Institute Inc. 1996), respectively.

RESULTS

Probability of active sheep fleeing and distance fled

When focal sheep were active prior to overflights (N = 51), 37% fled and 63% did not. Sheep ran during 84% of fleeing events (16 of 19), including 5 cases in which the focal animal alternated running and walking, and walked during only 3 observations. When fleeing, sheep took a median of 28 steps (maximum = 173, 25% quartile = 13, 75% quartile = 40, N = 15; excluding 3 cases in which sheep ran out of sight behind topography and 1 case in which the plane circled sheep). After the initial flight, sheep usually stood vigilant and then walked a few steps before bedding or feeding (total steps taken before bedding or resuming feeding: maximum = 183, median = 31, 25% quartile = 14, 75% quartile = 63, N = 15; 4 cases excluded as above).

According to the reduced logistic regression model ($Rho^2 = 0.20$; Table 1), fleeing probability for active animals depended on minimum distance from trajectory. Fleeing probability was 0.5 when the plane flew directly towards sheep (i.e. minimum distance from trajectory was 0 km), but decreased steeply as minimum distance from trajectory increased to about 0.7 km. No animals fled when minimum distance from trajectory was >0.7 km (Fig. 1).

Univariate analyses during preliminary stages of model building (Hosmer and Lemeshow 1989) did not detect effects of relative elevation (Wald tests for the Box-

Table 1. Reduced logistic regression model estimating fleeing probability by active sheep.

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	P
Intercept	0.91	-0.13	2.14	1.57	0.11
minimum distance from trajectory	-3.26	-6.52	-1.07	-2.33	0.02

N = 51 focal animal samples, Log likelihood = -33.68, Chi-squared = 13.57, DF = 1, P<0.001, $Rho^2 = 0.20$.

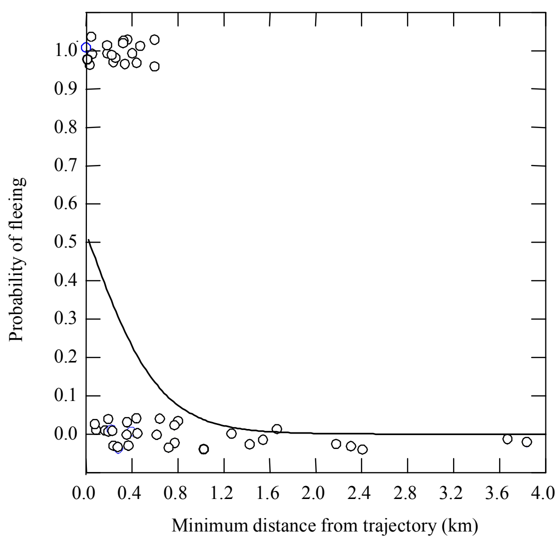

Fig. 1. Proportion of active sheep fleeing as a function of minimum distance from trajectory. The curve is the fleeing probability as estimated by the reduced logistic regression model of Table 1. Circles represent observed values and are jittered so that overlapping data points can be read.

Tidwell transformation [Hosmer and Lemeshow]: t = 0.32, DF = 1, P = 0.75). Distance from rocky slopes also did not enter the preliminary multivariate model (Wald test for univariate model: t = 0.99, df = 1, p = 0.32).

Probability of bedded sheep un-bedding

When focal sheep were bedded prior to overflights (N = 30), 53% remained bedded and 47% un-bedded. Of the latter, 57% (8 of 14) fled for 11-85 steps (median = 17, 25% quartile = 13, 75% quartile = 26, N = 8), while the remaining focal individuals stood vigilant or took <10 steps. After the initial flight, sheep that fled tended to walk further before re-bedding or feeding (total steps taken before resuming maintenance activities: maximum = 95, median = 52, 25% quartile = 17, 75% quartile = 87, N = 8).

According to the reduced regression model ($Rho^2 = 0.38$; Table 2), the probability of un-bedding decreased as minimum distance from trajectory and relative elevation increased (Figs. 2, 3). The model estimated that when the plane was 80 m above sheep (the median relative elevation for observations of bedded animals) or at smaller relative elevations, un-bedding probability was very high (>0.8) if the plane flew directly towards the animals, and that un-bedded probability remained >0.2 when distances were <1 km (Fig. 2). Un-bedding probability, however, was much lower when the plane flew higher above sheep, even when minimum distance from trajectory was short. For example, at 190 m above sheep (the 75% quartile), the probability was ≈0.4 when the plane flew directly towards sheep, but decreased to <0.1 at minimum distances from trajectory >0.8 km (Fig. 2).

I found no effect of distance to rocky slopes. This variable did not enter the preliminary multivariate model (Univariate Wald test during preliminary model building [Hosmer and Lemeshow 1989]: t = 0.88, df = 1, p = 0.38).

Table 2. Reduced logistic regression model estimating un-bedding probability by bedded sheep.

Variable	Regression coefficient			Wald test	
	Estimate	Lower 95% confidence limit	Upper 95% confidence limit	T-ratio	P
Intercept	2.81	0.95	5.39	2.56	0.011
minimum distance from trajectory	-2.66	-5.91	-0.58	-1.97	0.049
relative elevation	-0.016	-0.031	-0.0057	-2.49	0.013

N = 30 focal animal samples, Log likelihood = -20.73, Chi-squared = 15.76, DF = 2, P<0.001, Rho^2 = 0.38.

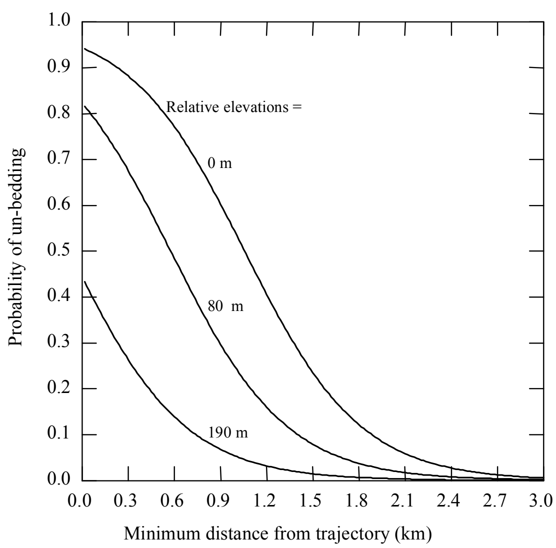

Fig. 2. Estimated probabilities of bedded sheep un-bedding as a function of minimum distance from trajectory and relative elevation. Curves were generated with parameters of the reduced logistic regression model of Table 2. Each curves represents, in descending order, a relative elevation of 0 m, 80 m (the median value), and 190 m (the 75% quartile).

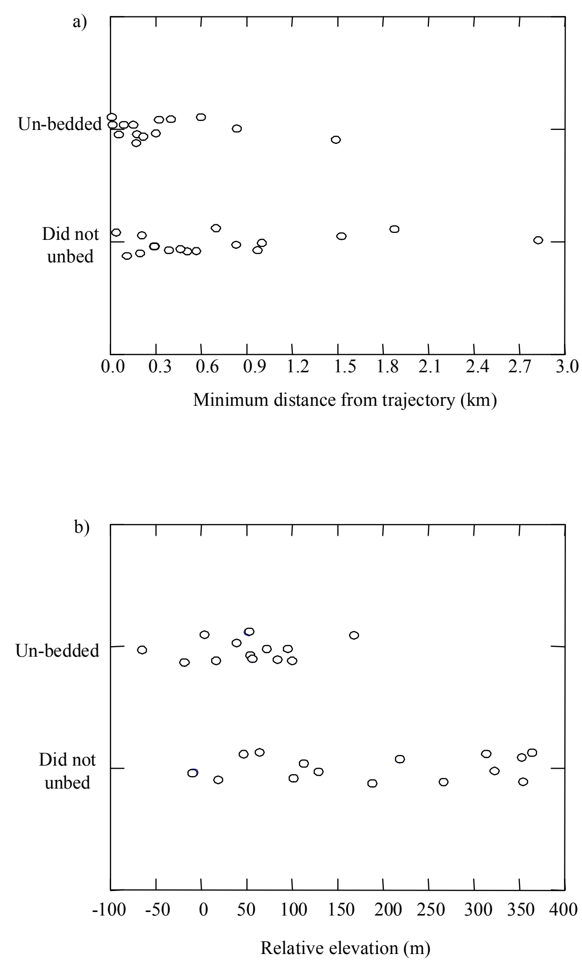

Fig. 3. Univariate scatterplots of the proportion of bedded sheep un-bedding in relation to (a) minimum distance from trajectory and (b) relative elevation. Figure is descriptive only because multivariate effects are not shown.

Time not feeding or bedded

Active sheep that showed an overt response towards the plane (either stood vigilant or fled) took a median of 31 seconds to bed or resume feeding (25% quartile = 14 s, 75% quartile = 46 s, range 2-149 s, N = 37; excluding 3 cases in which sheep ran out of sight behind topography and 2 cases in which then plane circled focal animals). According to the reduced regression model, the time to return to energy-gaining activities decreased as minimum distance from trajectory increased (Fig. 4: F = 10.55, DF = 1,35, P = 0.007, $R^2 = 0.19$). Relative elevation and distance to rocky slopes were excluded from the model.

Bedded sheep that un-bedded during overflights took a median of 86 seconds to begin to either forage or to re-bed (range = 16-370 s; 25% quartile = 67 s, 75% quartile = 124 s, N = 14), which was almost 3 times longer than for active sheep that showed a response (Mann Whitney U-statistic = 82, P <0.001). The time to begin feeding or to re-bed did not depend on minimum distance from trajectory (simple linear regression: t = -0.016, DF = 1, P = 0.99).

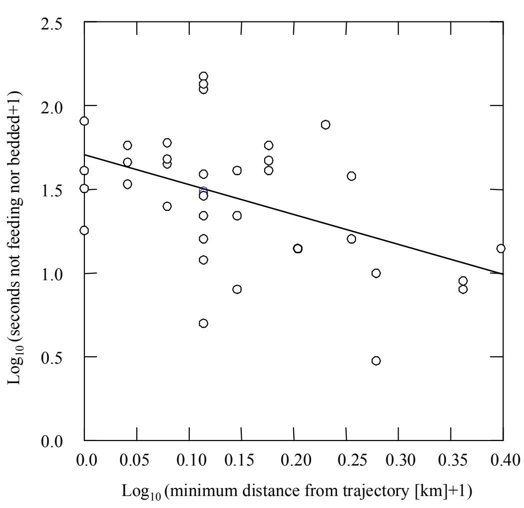

Fig. 4. Time not feeding or bedded by active sheep in relation to minimum distance from trajectory. Regression line is generated with the equation $y = 1.69 - 1.69x$ ($R^2 = 0.19$, see text).

Behaviour and time relative to overflights: foraging animals

Analyses described in this section are for active sheep. Because I was interested in the potential effect of overflights on energy-gaining activities, sheep which foraged for <50% of the pre-overflight period (who were travelling or engaged in social activities) were excluded from analyses.

Three of 8 focal individuals which fled during overflights bedded for 69% (1 sheep) or 91-100% (2 sheep) of the post-overflight period. In contrast, sheep that did not flee (N = 14) did not bed after overflights, except for 1 individual which bedded for the last 16 seconds of the post-overflight period.

For those individuals which did not bed during most or all of the post-overflight period, there was no substantial difference in time spent foraging before and after overflights (Fig. 5a), regardless of whether they fled or not (Wilcoxon signed rank test for sheep that fled: Z = 0.31, P = 0.75, N = 5; for sheep that did not flee Z = 0.47, P = 0.64, N = 14). There was also no difference in time spent moving during the pre- and post-overflight periods for these same animals (Fig. 5b: Wilcoxon signed rank test for sheep that fled: Z = -0.41, P = 0.67; for sheep that did not flee: Z = -0.40, P = 0.68).

Behaviour and time relative to overflight: animals that un-bedded

In the 7 samples of bedded sheep that un-bedded in response to the plane, 6 sheep were active for 44-100% of the post-overflight period. Specifically, the time spent bedded during the post-overflight period was 96% for 1 sheep, 48-56% for 2 sheep, and 0% for 4 sheep. Sheep which were active for at least 44% of the post-overflight period (N = 5) spent more time foraging (median = 45%) than vigilant (median = 8%) or walking (median proportion = 12%).

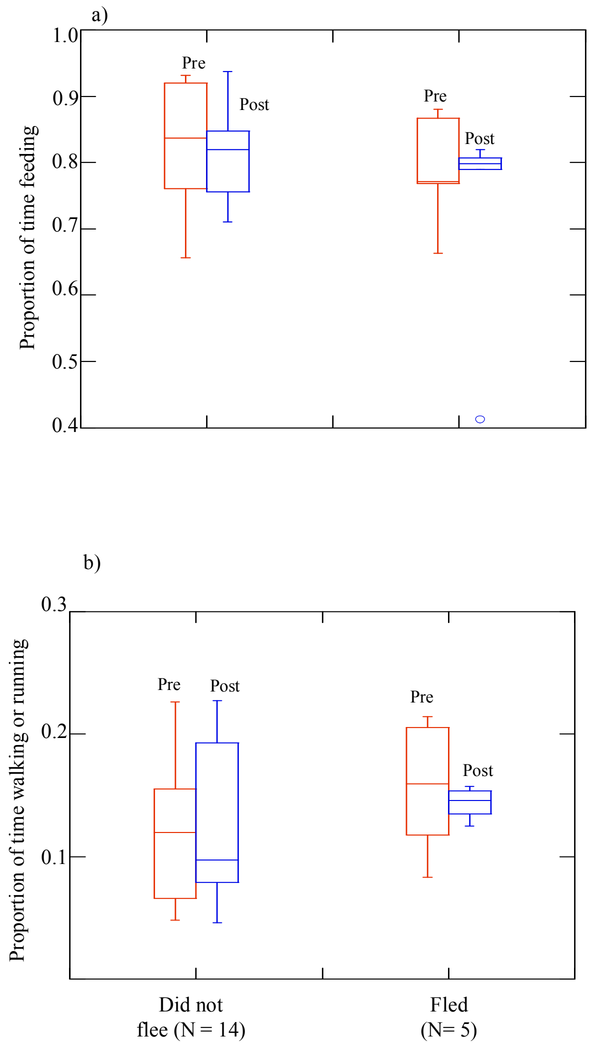

Fig. 5. Box plots of the proportion of time (a) feeding and (b) walking/running by active sheep during the 10-min periods that preceded and followed overflights. (These periods are marked on the figure as "pre" and "post" respectively.) Three sheep that were active before disturbance but which bedded almost immediately after overflights are excluded.) Boxes encompass 25% and 75% quartiles, the central line within the box represents the median, and the whiskers encompass 90% of the values. The circle in Fig. 5a represents a value outside the whiskers (see Wilkinson et al. 1996).

Fleeing responses to direct approaches in relation to cumulative weeks of overflights

Analyses presented here are limited to minimum trajectory distances of <0.6 km, which had a median value of 0.3 km during each week of the study (weeks 3 and 4 were pooled). There was no substantial difference in the proportion of active sheep fleeing during the 4 weeks of cumulative overflights (Fig. 6: Pearson Chi-square = 0.65, DF = 2, P = 0.72).

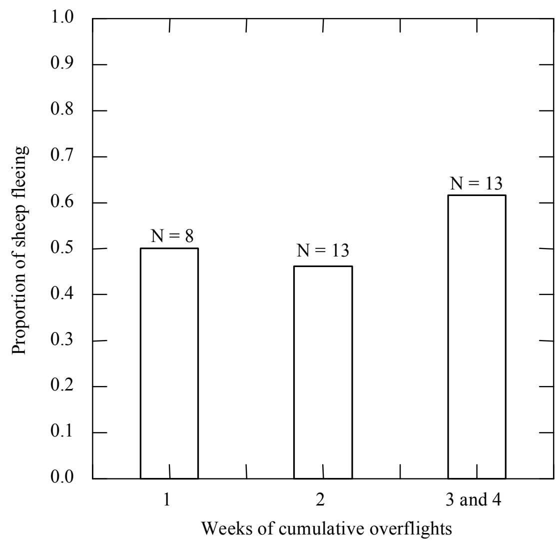

Fig. 6. Proportion of active sheep fleeing in relation to weeks of cumulative overflights. Data are shown only for overflights in which minimum distance from trajectory was<0.6 km (weekly median = 0.3 km).

DISCUSSION

Results supported the prediction that the probability of active sheep fleeing and of bedded sheep un-bedding would increase as the plane's angle of approach became more direct. These results are consistent with observations of mountain Caprinae exposed to helicopter overflights (Côté 1996, Frid 1999*a*) and bighorn sheep (*O. canadensis*) disturbed by fixed-wing aircraft (Krausman and Hervert 1983), and with tests of economic models of prey fleeing from predators (Burger and Gochfeld 1981, 1990;

Cooper 1997, 1998; see Bulova 1994 for an exception). Angle of approach affected un-bedding probability in both a horizontal and vertical plane, as indexed by minimum distance from trajectory and relative elevation, respectively. There was no significant statistical interaction between these two variables, however, indicating that within the range of distances and elevations analyzed the vertical and horizontal components of angle of approach affected un-bedding probability independently. Relative elevations below –60 m were not considered by the model of un-bedding probability because of limited sample sizes at that part of the distribution. Observations of very low relative elevation are difficult to obtain at my study area because the complex topography would jeopardize pilot safety; future work at a site with safer flying conditions should test the hypothesis that the effect of relative elevation is an inverse U-shape function, with animals not interrupting resting bouts at very high and very low relative elevations. (Preliminary analyses which were marginally not significant suggested that was the case.) For fleeing probability, I detected an effect of angle of approach only in a 2-dimensional plane, possibly because sample sizes of very high relative elevations were inadequate (they were smaller than for the un-bedding probability model).

The prediction that the time that disturbed sheep did not feed or bed would increase as approach directness becomes greater was supported for active sheep, and results agreed with observations of mountain goats (*Oreamnos americanus*) disturbed by helicopters (Côté 1996). It is also consistent with studies testing the hypothesis that prey respond more strongly to predators approaching more directly (Burger and Gochfeld 1981, 1990; Cooper 1997, 1998.) (The prediction was not supported for bedded sheep, but sample sizes were low.) As in the case of fleeing probability, only the horizontal component of angle of approach had an effect, possibly because of the limited distribution of relative elevations.

Contrary to my prediction, I found no effect of distance to rocky slopes on any response variable. These results contrast sharply with my observations of helicopter disturbance of the same sheep population during 1997, when I found that the effect of minimum distance from trajectory on fleeing probability depended on the sheep's distance to rocky slopes. Fleeing probability decreased as minimum distance from trajectory increased, but did so at a higher rate for sheep that were on or near rocky slopes than for sheep farther from rocky slopes (Frid 1999*a*). While the lack of effect of rocky slopes in relation to fixed-wing overflights could reflect inherent differences between aircraft types, that possibility cannot be evaluated by my study because distance to rocky slopes was significantly smaller (Mann-Whitney U test statistic = 1394.5, $P < 0.001$) for the focal individuals observed in this study (median = 1 m, 25% quartile = 0 m, 75% quartile = 10 m, N = 81 focal animals) than for the focal groups observed during the helicopter disturbance study (median = 20 m, 25% quartile = 0 m, 75% quartile = 93 m, N = 56 focal groups).

My prediction that bedded sheep which interrupted resting bouts during overflights would spend less time bedded after overflights was supported; only 1 of 7 sheep re-bedded for the post-overflight period, and only 2 additional sheep re-bedded for >1% of this period. Disruptions of bedding activity could affect rumination and energy assimilation (review in Maier 1996), and thus are a conservation concern. Results were consistent with my observation that when sheep were disturbed by helicopters, on average, 6-10 min after overflights the mean proportion of bedded sheep in a group was half of the pre-disturbance proportion and, though not significantly, 11-20 min after overflights the mean proportion of bedded sheep was two thirds of the pre-disturbance proportion (Frid 1999*b*). They are consistent also with studies testing the hypothesis that prey remain alert after a predator encounter because of the possibility of further attack (review in Lima and Dill 1990).

My prediction that sheep would feed less efficiently and move more after overflights than prior to them was not supported for active sheep. After overflights, some individuals bedded while others fed for a proportion of time that was similar to that of the pre-overflight period and to that of sheep that did not flee. These results suggest that each disturbance event caused a low energetic cost to active sheep. (It is interesting that several active sheep that fled bedded after disturbance; I observed a similar pattern during the helicopter disturbance study [Frid 1999*b*]).

I did not find evidence of habituation; when minimum distance from trajectory was <0.6 km, ≥46% of active sheep fled during each week of cumulative observation, with the highest proportion (62%) occurring during the last 2 weeks of the study. While data did not support the hypothesis that animals should habituate to non-lethal human disturbance, thus avoiding unnecessary investments in antipredator behaviour (Burger and Gochfeld 1981, 1990), my study may have been too short for a proper test. Multi-year research on helicopter disturbance, however, concluded also that bighorn sheep did not habituate substantially to overflights (Bleich et al. 1994). Thus, the potential effect of aircraft disturbance on sheep conservation remains a concern.

Conservation implications

While behavioural responses tended to be short-term, rigorously designed experiments (see Underwood 1994) and/or energetic models (see Bradshaw 1994; Luick et al. 1996; White 1999) have yet to determine whether a high-rate of fixed wing overflights can affect the reproductive success and population dynamics of mountain sheep. An energetic model was beyond the scope of this paper, yet my results provide some parameters (e.g. steps taken and time lost from foraging and rumination) needed for that model.

Once the disturbance rates which affect fitness are estimated theoretically, models of fleeing and un-bedding probability as a function of minimum trajectory distance and relative elevation could be used to generate restrictions on aircraft trajectories and maintain disturbance within acceptable levels. I suggest that these restrictions be based on un-bedding rather than fleeing probability. While active animals tended to resume foraging shortly after the plane left the area, most sheep that un-bedded during overflights did not re-bed afterwards. This was the case also during my study of helicopter disturbance (Frid 1999*a*). Furthermore, sheep that un-bedded tended to take almost 3 times longer than active sheep that fled to begin to feed or to re-bed. The potential consequences of disturbance could be more substantial in terms of lost rumination time rather than in terms of lost foraging time and locomotion costs (see Maier 1996). As illustrated by Fig. 2, the model of un-bedding probability also allows restrictions on minimum trajectory distance to be relaxed when the plane is flying high above sheep.

The logistic regression models I present here should be used with caution. They explain only 20-38% of the variability in responses, and confidence limits (Tables 1, 2) should be heeded. Also, models are restricted to sheep under the conditions that I observed them in: during the weather and plant phenology of the particular field season, near rocky slopes, etc. Spatial and temporal replication are needed to increase the generality of my models.

I must emphasize also that my data do not quantify responses in relation to overflights in which the plane circled over sheep. These types of trajectories are much more disturbing to sheep (Frid unpublished data) and should be addressed by future work.

My findings were consistent with other work suggesting that fixed-wing aircraft was less disturbing to sheep than helicopters (Bleich et al. 1994). For example, when minimum distance from trajectory was <0.6 km, 100% of sheep (N = 25) fled during helicopter overflights, regardless of whether sheep were on rocky slopes (thus less likely to flee) (Frid 1999*a*). In contrast, during fixed-wing overflights in which minimum distance from trajectory was <0.6 km, only 53% of 34 active sheep fled and only 58% of 19 bedded sheep un-bedded. Thus, I suggest that wildlife managers should encourage commercial operations (mining, tourism, etc) occurring in roadless sheep ranges to use fixed-wing aircraft rather than helicopters whenever landing requirements allow.

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