

IMPACTS OF HUMAN ACTIVITY ON BIGHORN SHEEP IN
YELLOWSTONE NATIONAL PARK

by
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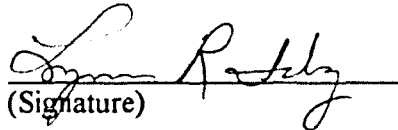
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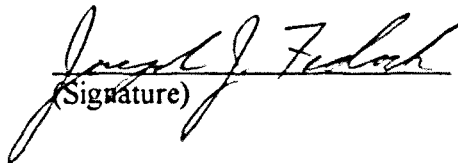
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ABSTRACT

Seventeen years have passed since bighorn sheep (*Ovis canadensis canadensis*) in Yellowstone National Park (YNP) experienced a massive *Chlamydial*-caused die-off. Currently, no sign of *Chlamydia* or pneumonia is evident, thus other factors are considered to be limiting the population. The proposed changes to the Gardiner-Mammoth highway and the highway through Dunraven Pass could increase or decrease human disturbances to the core population of bighorn sheep. Approximately 65 % of all observations on the Everts winter range occurred on the top of McMinn Bench (along the proposed road route). One ewe group currently must cross the Gardiner-Mammoth highway to reach spring lambing grounds. The placement of the road onto McMinn Bench would impact at least 2 other populations of ewe groups and 2-3 populations of ram groups, which seek shelter, security, water, and minerals in the cliffs. Use of the Dunraven Pass road corridor was low and potential displacement from road changes would be minor. Disturbance events were recorded during behavioral observations. Human presence was recorded for 26 % of all observations, with 25 % of these resulting in disturbances. The percentage of overall human disturbances for all observations in each group was: McMinn Bench ewes 7.5 %, McMinn Bench rams 4.6 %, Mount Washburn 4.3 %, Deckard Flats 5.4 %, Rattlesnake Butte 2.9 %. The most disturbing human activity (based on overt reactions) was helicopter aircraft. To evaluate the effects of these human disturbances I used 3 non-invasive techniques that may be indicators of stress in bighorn sheep: behavioral activity levels, lungworm larvae shedding levels (LPG), and levels of the hormone corticosterone. Most groups were not significantly different in degree of activity except for McMinn Bench, which had higher levels of activity than Rattlesnake Butte. Significant differences were found in LPG between sexes (rams < ewes) ($F = 4.76, P = .0299$) and between two groups (McMinn Bench < Rattlesnake Butte) ($F = 7.24, P = .0075$). LPG did not correspond to levels of disturbance or degree of activity. Corticosterone levels did not correlate with LPG levels, suggesting that LPG may not be a good indicator of disturbances. Corticosterone differences in radio-collared and uncollared individuals were insignificant. Rams had significantly lower corticosterone levels than females ($F = 4.56, P = .0334$). Levels dropped during winter and increased dramatically for both rams and ewes during the month of May, suggesting that measures of corticosterone may be more indicative of social stress than climatic or nutritional stress during the winter. McMinn Bench ewes had significantly higher levels of corticosterone than Rattlesnake Butte ewes ($F = 6.31, P = .0125$) corresponding with distance to road, activity levels, human disturbance rates and possibly reproductive success.

INTRODUCTION

Prehistoric evidence indicates that aboriginal man hunted bighorn sheep in the Greater Yellowstone Area for at least 8,000 years (Lahren 1971). Historically, Rocky Mountain bighorn sheep were found in all mountain ranges in and around Yellowstone National Park (YNP) (Mills 1937). Market hunting in the 1870's had a dramatic impact on ungulates, reducing or eliminating many populations during the 1880's and 1890's (Houston 1980). The establishment of YNP in 1872 and, more importantly, the movement of the U.S. Army into the park in 1886 helped preserve the population of bighorn sheep on the Mount Everts winter range (EWR). Bighorn sheep in and adjacent to the northern boundary of YNP are organized into 8 or more groups. The probable genetic linkage among groups, as indicated by movement data (Martin 1980, Keating 1982, Legg 1996, Irby 1994), suggest that these groups operate as a metapopulation (Soule 1986).

Between 1894 and 1910, approximately 1,500 people inhabited the coal mining towns of Electric and Aldridge. Intensive human activity, unregulated hunting, habitat degradation, and disease transmission from domestic livestock probably caused the demise of the Cinnabar mountain population of bighorn sheep directly north of the park boundary (Keating 1982). This served to isolate the EWR population until around 1965, when this population experienced an exponential growth phase resulting in the emigration and recolonization of the population on the CWR (Keating 1982). This recolonization and expansion of existing populations occurred 20-30 years after land use

patterns changed, hunting was regulated, and livestock in the region was better managed (Keating 1982, Irby et al. 1989, Legg et al. 1996).

It was not until the 1960's that efforts were made to better understand and study the status and distribution of bighorn sheep in and around YNP. Annual reports contain incomplete information about population levels in the early 1900's. Prior to 1958, surveys were conducted in conjunction with other activities and are only useful for rough estimates of the population. Extensive aerial surveys (both fixed wing and helicopter) have been conducted almost every year since 1958 (Barmore 1980, Caslick 1993, Lemke MFWP report 1996). During the summer of 1966, the first attempt was made to conduct a bighorn sheep survey that included all of YNP, with the exception of the Bechler Canyon region. A total of 558 bighorn sheep were counted with 346 of these in the northern third of YNP. Since then, counts of bighorn sheep populations on the northern winter range of YNP have ranged from a high count of 487 in 1981 to a low of 134 in 1998 (Meagher et al. 1992; Caslick 1993; Lemke 1998, Unpublished Report, Montana Fish, Wildlife and Parks, MFWP). The same general trend has been seen with the bighorn sheep that are associated with the EWR. (Fig.1).

During the winter of 1981-1982, an outbreak of infectious keratoconjunctivitis resulted in the mortality of approximately 60 % of the total northern range population and up to 80 % of the EWR population (Keating 1982, Meagher 1982, Legg 1996, Meagher et al. 1992, Caslick 1993). Seventeen years later the population has not shown significant signs of recovery and may be decreasing. Bighorn sheep populations to the north and east of the EWR have also declined (Lemke MFWP Reports 1987-1998, Legg 1996).

Recent studies found that human disturbance, poaching, inbreeding, disease, and interspecific competition were unlikely to be important in limiting populations north of the YNP boundary (Irby et al. 1986, 1989, Legg 1996). Evidence suggests that populations both in and outside YNP experience very different levels of predation, interspecific competition and human disturbance. Therefore, the disturbing question is why populations are declining both within the protection of YNP and outside the boundaries.

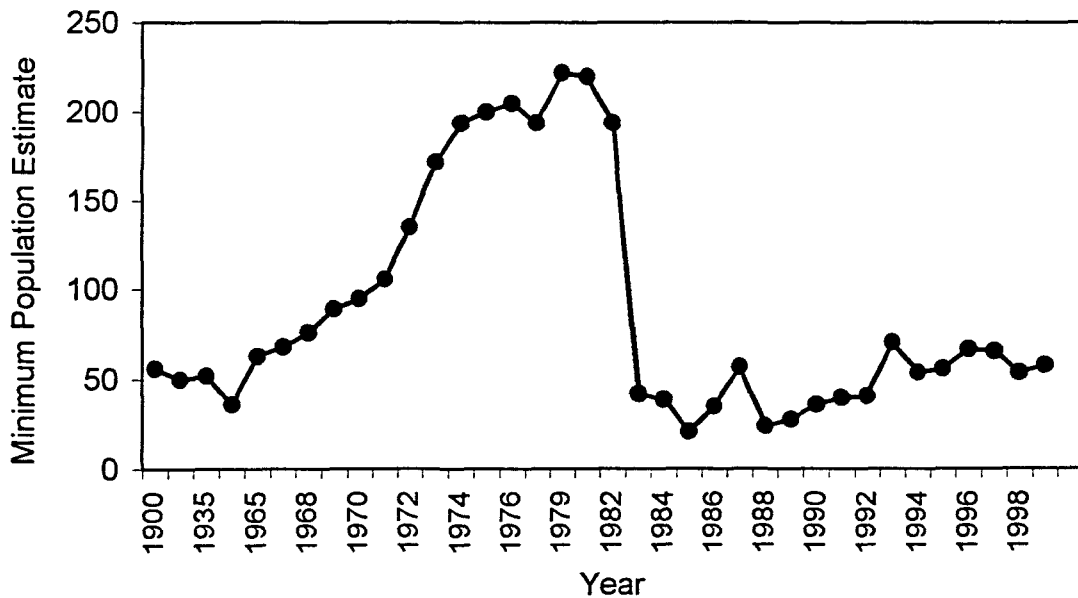


Figure 1. Long term population trend data on the Everts winter range. Compiled from Keating (1982), Caslick (1993), Meagher et al. (1992), and Lemke (1998).

This study was begun in order to evaluate the potential impacts of the proposed realignment or movement of the Gardiner-Mammoth highway and the highway through Dunraven Pass. There were fears that changes in these roads, which currently run

through bighorn sheep habitat, could exacerbate conditions faced by a population with questionable recruitment capabilities. This was the first study to utilize bighorn sheep collared within YNP and was, therefore, important in establishing baseline information on the timing of movements, specific migration corridors, and behavior. Noninvasive means were utilized (behavioral observations, lungworm counts in feces and fecal corticosterone levels) to assess human disturbance on bighorn sheep.

The specific objectives were to:

- 1) Determine migration routes, lambing sites, high use areas, and watering sites associated with sheep using the EWR.
- 2) Determine if groups associated with the EWR were exposed to different levels of disturbance from humans. If so, did stress (as indicated by behavior, fecal corticosterone levels, and lungworm shedding) differ in relation to levels of human disturbance.
- 3) Develop recommendations for road construction activities and alignments that would result in the least disturbance on the EWR population of bighorn sheep.

The following null hypotheses were tested for groups exposed to different levels of human contact.

H₁: There is no difference in lungworm shedding levels among groups.

H₂: There is no difference in behavioral activity among groups.

H₃: There is no difference in fecal corticosterone levels among groups.

STUDY AREA

The Mount Everts Winter Range

The EWR is comprised of approximately 480 ha at 1500-2000 m in elevation. It is located south of Gardiner, Montana at the confluence of the Yellowstone and Gardner Rivers (Fig. 2). Bighorns which winter on the EWR congregate for breeding, which takes place in November and December, and remain in the area until lambing in May.

Most of the topography dates to the Pleistocene or Holocene and is composed of mudflows, stream cut terraces, breaks, and glacial moraines. Soils have been forming since periglacial and pre-glacial periods, from landslides, stream alluvium, glacial outwash and till, weathered travertine, and weathered shale and sandstone. Some areas have high sodium and clay contents that may limit plant productivity (Shovic et al. 1991).

The climate is relatively warm and dry when compared to the rest of YNP (Houston 1982). Weather patterns are locally influenced by the topography of the region, often with very different levels of precipitation within several kilometers. Winds tend to be strong and keep southwest facing slopes and ridges free of snow during the winter months.

Habitat types in YNP are described in detail by Despain (1990). On the EWR the grasslands are composed of primarily 2 or 3 habitat types: Idaho fescue (Festuca idahoensis)-blue-bunch wheatgrass (Agropyron spicatum), and sage (Artemesia tridentata) mixed with both bluebunch wheatgrass and Idaho fescue. Scattered woodlands are found on higher elevations and drainages of the EWR and include several

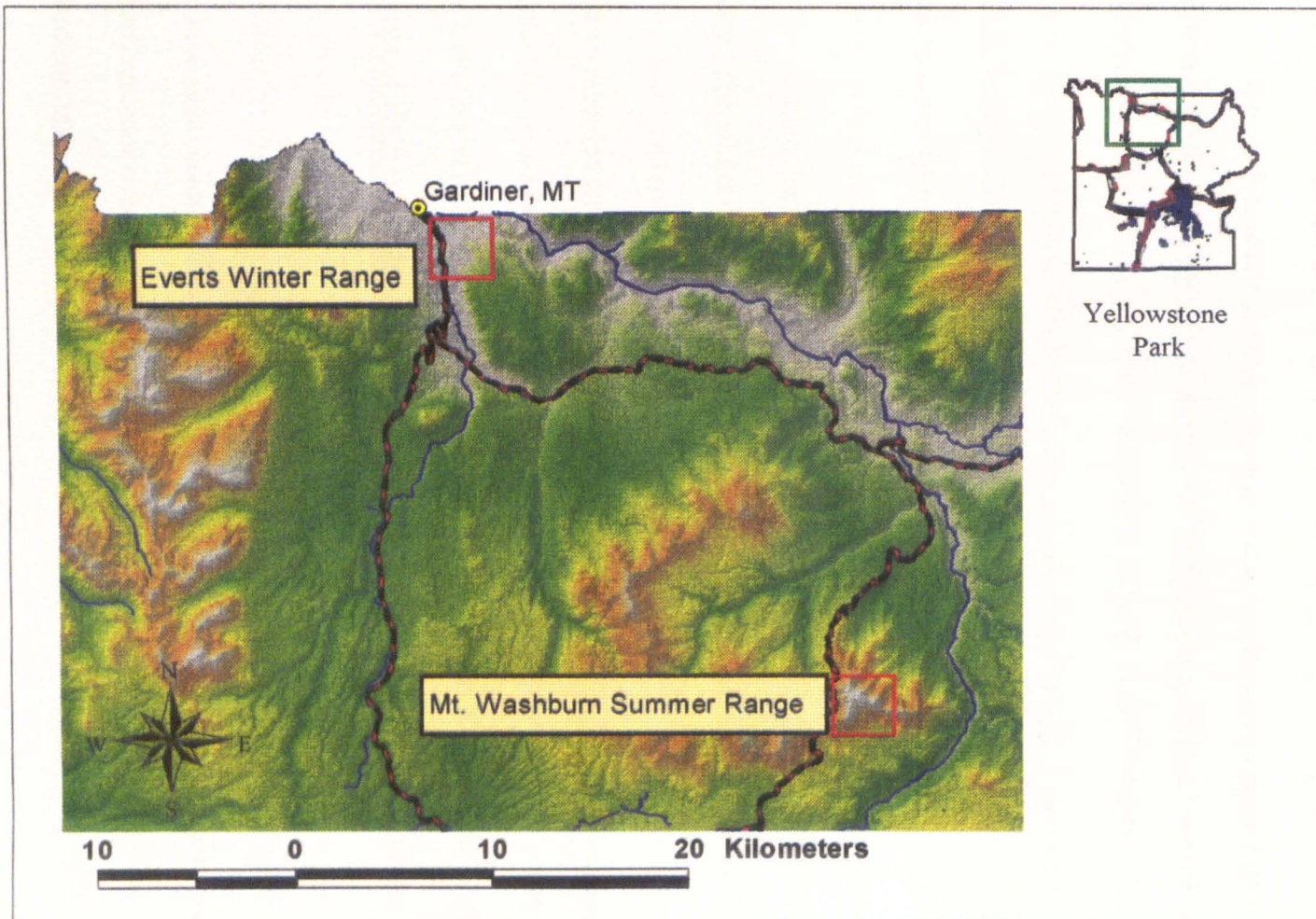


Figure 2. Study area boundary with core study sites for winter and summer identified in red.

Douglas-fir (*Pseudotsuga menziesii*) habitat types (Despain 1990). Exotic herbaceous plants are common in the grass and shrub communities as a result of past disturbances.

The EWR is within the main migration route for elk (*Cervus elaphus nelsoni*), mule deer (*Odocoileus hemionus*), pronghorns (*Antilocapra americana*) and bison (*Bison bison*) on the northern range in YNP. Numerous predators capable of killing sheep also use the area, including, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), coyotes (*Canis latrans*), wolves (*C. lupus*), mountain lions (*Felis concolor*), bobcats (*F. rufus*) and golden eagles (*Aquila chrysaetos*). The extent that these species use the EWR, and the resultant interspecific competition and predation, depends on the severity of the winter.

During this study, summer and winter weather differed significantly between years. The winter of 1996-1997 was one of the harshest on record for YNP based on snow pack conditions, accumulation, and temperatures. However, the Gardiner weather station recorded minimum and maximum temperatures and snowfall that were very close to the 30-year average (Fig. 3). The following summer of 1997 was very wet with precipitation well above normal for the months from May through September. The winter of 1997-1998 was a mild winter with below average precipitation and was followed by a hot dry summer (Fig. 4). The difficulty in determining variations in weather in mountainous regions is exemplified by the precipitation records for the month of June 1998. Records from two weather stations which border the study area (only 8 km apart) recorded over 17 cm of rain and under 1 cm of rain in Mammoth, WY and Gardiner, MT, respectively.

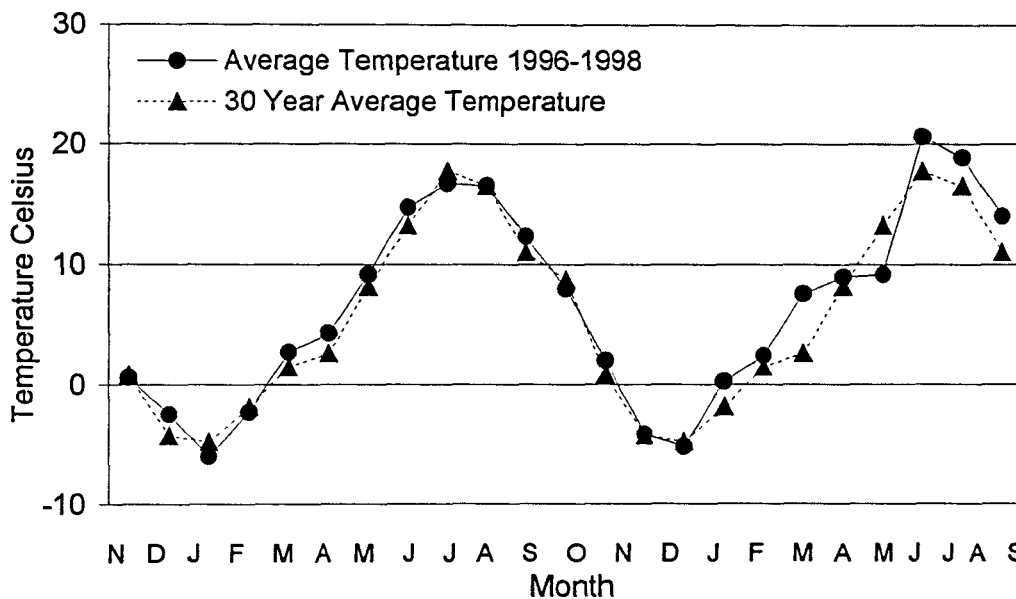


Figure 3. Comparison of the 1996-1998 mean monthly temperature versus the 30 year mean monthly temperature. Compiled from NOAA weather stations in Gardiner, MT and Mammoth, WY.

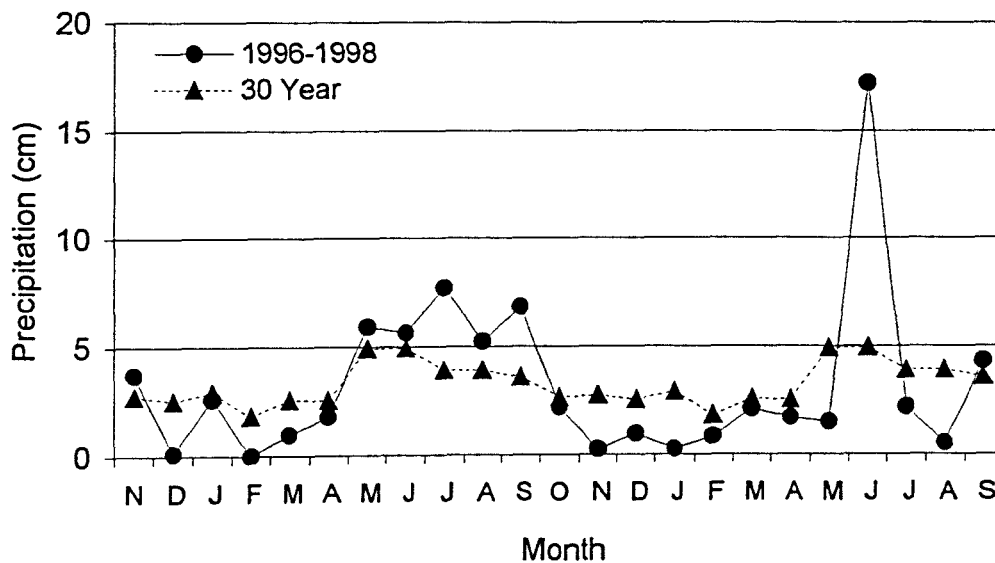


Figure 4. Comparison of monthly precipitation from 1996-1998 versus 30-year means. Compiled from the NOAA weather stations in Gardiner, MT and Mammoth, WY.

Summer Ranges Associated with the EWR

The bighorn sheep that winter on the EWR exhibit varying degrees and distances of seasonal migrations. Forest habitats associated with migration routes and upper elevation summer ranges are composed of subalpine-fir (Abies lasiocarpa), Engelmann spruce (Picea engelmannii), and whitebark pine (Pinus albicaulus) (Houston 1982). Summer temperatures on Mount Washburn averaged 9.2 C in 1997 and 8.6 C in 1998 for the months of July and August. Precipitation ranged from 8.9 cm (1997) to 15.2 cm (1998) for the same two months. High elevation summer ranges (above 3,300 m) are often classified as alpine tundra habitat characterized by a thick mat composed of numerous grass and forb species. Some of the most common grass species are sheep fescue (Festuca ovina), timberland bluegrass (Poa rupicola), Cusick's bluegrass (Poa cusickii) and Sandberg's bluegrass (Poa sandbergii), with forbs including silvery lupine (Lupinus argenteus), arctic sandwort (Arenaria obtusiloba) and lance leaf stonecrop (Sedum lanceolatum). Buechner (1960) thought that the only true alpine meadow in YNP was above timberline on Mount Washburn. Further details of habitat types are described in detail by Despain (1990), and information on long term climatic cycles can be found in Houston (1982).

Bighorn sheep shared summer ranges with most of the same potential competitors and predators found on the winter range but at apparently lower densities. Differences in habitat quality and levels of predation and competition may explain alternate strategies employed by groups of animals that share the same winter range. Migration strategies in YNP have been described as complete, semi-migratory, and non-migratory. Greer (1931)

found bighorn summer ranges were only an enlargement of their winter range, while Mills (1937), Davis (1938), and Gammill (1941) reported that migrations in YNP appeared “incomplete or short.” In these early studies, specific movements of bighorn sheep bands proved difficult to verify and accurately track since radio-collared animals were not available. More recently, studies that utilized aircraft to simultaneously monitor movements of many groups of bighorn sheep allowed researchers to discover that there are a variety of migration strategies in YNP. Oldenmeyer (1966) and Woolf et al. (1970) concluded that some populations exhibited typical long distance migrations while other populations merely enlarged their use around the winter range habitat.

Fire historically played an important ecological role in YNP. Fire suppression has been shown to negatively impact habitat quality for bighorn sheep in many regions due to conifer encroachment (Riggs and Peek 1980, Schirokauer 1982). Scarred trees indicate fires were frequent on the steep slopes along the Yellowstone River between Quartz Creek and Deep Creek, in the Black Canyon from Bear Creek to Hellroaring Creek and on the Gardiner River from Lava Creek to Osprey Falls (Houston 1982). Recent fires near Mount Washburn and Sepulcher Mountain burned significant stands of conifers that are now frequented by bighorn sheep.

METHODS

Capture and Handling

Fourteen ewes and 4 young rams (1-3 year olds) were captured, aged, and radio-collared utilizing Advanced Telemetry Systems collars fitted with cotton spacers to allow the collars to release without recapturing the animals. Blood, nasal swabs, ear tissue plugs (for future genetic work), and fecal samples were also collected. Personnel from Helicopter Wildlife Management Inc. captured the majority of animals in March using helicopters and net guns. Two other animals were immobilized with carfentanil from the ground in September by personnel from YNP and NWF (Andryk et al. 1983, Bates et al. 1985, Kock et al. 1987, Heimer et al. 1990). Montana State Diagnostics laboratory at Montana State University conducted the serological tests on the blood and ran cultures of the nasal swabs to be tested for antibodies.

Movements and Behavior

Collared bighorn sheep were used as focal subjects of groups that were located daily during the winter and 2-3 times a week during the summer on random days and categorized time periods. Groups migrating from winter to summer ranges were located by air with a Piper Super Cub and then tracked by foot using a hand held H-antenna. All locations were entered into a Geographic Information System (GIS) and the program CALHOME (utilizing the adaptive kernel method at 95 %) (Kie et al. 1994) to determine home ranges, areas of high use by bighorn sheep, migration corridors and areas with potential road realignment conflicts.

Once focal animals were located, individual behavioral data were recorded every 30 seconds during a 10-min observation period. Group data were also recorded, including information on overall group behavior, size, composition, distance moved, spread of the group, distance to other species, habitat features and distance to human activity. The mean time spent engaged in each activity was calculated for each individual and then pooled by season and group. Behavior was then classified as active or inactive to test for differences in individuals, groups, season, and time of day. Due to the repeated sampling nature of the study design, we used the Statistical Analysis System (SAS 1995) PROC – MIXED program to analyze the data.

Lungworm Analysis

Fecal samples were collected from known individuals at 1-month intervals for a period of one year. These samples were analyzed for levels of larvae from the nematode (Protostrongylus sp). I was able to increase the sampled individuals to approximately 50 % of the females and 23 % of the males plus 25 % of the class III and IV rams, by sampling other individuals with identifiable physical features and from identifiable age classes. Using these methods, a total of 388 fecal samples were collected over 12 months.

The standard technique for determining lungworm shedding levels is the Baermann analysis devised by Baermann (1917) and refined by Uhazy et al. (1973) and Beane and Hobbs (1983). There are numerous variations in the application of the Baermann technique that makes results inconsistent (Beane and Thompson 1983). This

relates to the method of storage of the pellets (dried at room temperature, refrigerated or frozen), the handling technique (crushing or not crushing), funnel material and size (glass or plastic), and time they are allowed to soak (from 8- 48 hours) (Beane and Thompson 1983, Forrester and Lankester 1997a). The techniques used, replicated as closely as possible the techniques previously used in the Yellowstone region in order to compare results to those from other studies. The samples were stored frozen < 2 months, not crushed and soaked for a period of 24 hours utilizing 10-cm plastic funnels.

The Baermann technique estimates the number of first-stage larvae per gram of dry feces (LPG). One major problem with the Baermann technique is entrapment of larvae on the sloping sides of the funnel. Up to 67 % of the larvae can be trapped resulting in false negatives and low counts. The larvae that are counted often do not correlate with the total number found in the feces. Forrester and Lankester (1997a) devised a new technique utilizing a beaker that eliminates the problems associated with the type and size of funnel used. This method has larval yields 8 times higher than the Baermann technique resulting in fewer false negatives and recovering > 91 % of the total numbers of larvae present (Forrester and Lankester 1997b).

Simultaneous Baermann and Beaker tests were run with all fecal samples in order to compare results to historical data and to test the correlation between the two techniques. While there is no mention in the literature of diurnal fluctuations in lungworm output, sheep were only sampled during the middle hours of the day.

Samples of 2.5 - 5.0 grams of semi-dried pellets were weighed and crushed, enclosed in tissue paper, stapled within a vinyl screen, and then suspended in a 250-ml

beaker filled with water for 24 hrs. The water was then siphoned off and the last 50-ml examined in a Petri dish for lungworm larvae. The number of larvae/gm of dried feces = the number of larvae collected from the sample/ [fresh weight of the sample * (dried weight of the subsample/initial weight of the subsample)].

A further complication in comparing results from previous lungworm analysis in the Yellowstone region is the treatment of the data. Some studies merely calculated the mean level of infection in a population, while others have transformed the data using natural logarithms or other techniques and then compared the means (Keating 1982, Arnett et al., 1993, Jones and Worley 1994). Festa-Bianchet (1991) found that a square-root transformation (tLPG) most closely approximated a normal distribution and that transforming the data using natural logarithms resulted in significant negative skew. Results with transformations were similar to those found by Festa-Bianchet, but I found a better fit using a cubed root transformation. The PROC- MIXED program was used to correct for repeated measures and test for significance. Regression analyses were run to determine the relationship between the Beaker and Baermann methods in evaluating infection rates. In addition, the prevalence of false negatives recorded by the Baermann method was compared to that found by the Beaker method. For all other analyses the more accurate Beaker method was used for calculating the mean tLPG levels for all collared animals and the mean tLPG for each group, sex, and age class.

Corticosterone Analysis

Sub-samples of feces used for corticosterone analysis were stored frozen at -40 C and were taken from the same samples that were collected for lungworm analysis. Time of defecation, location of the individual animal, and the group to which it belonged was recorded. To reduce the effects of diurnal periodicity in corticosterone levels, samples were collected during the middle of the day. From these frozen samples approximately 2.5 grams were removed and lyophilized in a Savant Instruments Speedvac Rotary Evaporator (Forma Scientific, Marietta, OH 45750, U.S.A.) for 5 - 8 hrs until completely dry, as determined by weight changes in feces during trials. Fecal sample processing and extraction procedures were modified from previously described methods (Wasser et al. 1991, 1994, Monfort et al. 1993, Brown et al. 1994, Schwartz et al 1995). Once dry the samples were pulverized and 0.18-0.21 g of powder were boiled in 10 ml of 100 % ethanol for 20 min; 3,000 d.p.m. radiolabeled ³H-corticosterone (New England Nuclear, Wilmington, Delaware 19860, USA) was added before extraction to monitor procedural losses and recovery using a quench curve compensation program. After centrifuging (500g for 15 min), the supernatant was decanted into a clean tube (16 x 125 mm) and dried under a stream of compressed air. As samples evaporated, vessel walls were rinsed twice with ethanol (4 ml per rinse) before the supernatant was evaporated completely and redissolved in 1-ml methanol. To complete the extraction procedure, tubes were vortexed (1 min), placed in an ultrasonic glass cleaner for 30 sec to free particulates adhering to the vessel wall, and then vortexed for 15 sec. Procedural losses, quantified by counting 25 µl of the final extractant, averaged $81.4 \pm \text{SE } 0.5 \%$ (n = 385 samples).

A double-antibody ^{125}I RIA for corticosterone (ICN Biomedicals, Inc., Costa Mesa, California 92626, U.S.A.) was validated for extracted bighorn sheep fecal extracts. According to the manufacturer, the antisera crossreacts with corticosterone (100 %), deoxycorticosterone (0.34 %) testosterone (0.10 %) cortisol (0.05 %) aldosterone (0.03 %), progesterone (0.02 %) and less than 0.01 % for all other steroids tested. Assays were used according to the instructions provided except that all reagent volumes were halved. Fecal extracts were assayed (1:2 in steroid diluent, 50 μl) as described previously (Monfort et al. 1998). Briefly, serial dilutions (range = undiluted-1:8) of pooled fecal extracts from randomly selected female and male bighorn sheep yielded displacement curves parallel to the standard curve. Mean recovery of added corticosterone (range, 25-500 ng / ml) was $108.0 \pm 15.9 \%$ ($y = 0.82 + 11.6, r^2 = 0.99$) and $90.3 \pm 6.5 \%$ ($y = 0.86x - 1.2, r^2 = 0.99$). Inter-assay coefficients of variation for two separate internal controls were 9.5 % ($n = 7, 23\text{-}30 \%$ binding) and 13.2 % ($n = 7, 57\text{-}72 \%$ binding). Intra-assay coefficients of variation were $< 5 \%$, and assay sensitivity was 25 ng / ml. All hormone concentrations are expressed as mass units of hormone excreted per gram of dry feces. The PROC-MIXED program was used in statistical analyses after the data was log transformed.

RESULTS

Capture and Handling

Few studies report results involving capture and handling techniques. In recent years capture techniques for ungulates have improved, reducing the risk of injury to both the target animal and humans. Many studies have compared the efficiency of net gun captures and drug immobilization from helicopters and found net-guns to be more cost effective as well as drastically reducing the risk of injury to bighorn sheep (Barrett 1982, Andryk et al. 1983, Kock 1987, Krausman 1985, Heimer 1990).

Capture myopathy (CM) is a condition that occasionally results through capture related stress to animals (Andryk et al. 1983). Stress or compromise in wild animals results in the alteration of certain biological parameters that can lead to death or permanent injury. Capture myopathy can develop if the level of stress is sustained and the animal is unable to adapt. The prevention of CM can best be attained through quick and efficient handling and chase times. Several studies have found bighorns to have slightly higher levels of capture mortality than other ungulates (approximately <3 %) (Kock et al. 1987). This higher level may be attributed in part to capture techniques that prolong periods of stress on the animals involved. Capture mortality should prove to be < 1 % in an operation handled in an efficient manner (Krausman et al. 1985).

A professional animal handling company captured the majority of the bighorn sheep in this study. A single Hughes 500C was used with handlers firing hand held net-guns. Handling times averaged about 8 min from the time the net was fired to the release of the animal. Employing professional animal handlers reduces the amount of time each

animal is handled as well as the total amount of time spent in the capture area. Fifteen bighorn sheep were captured within 3 hrs. One female, approximately 6 years of age, showed signs of severe capture myopathy and was euthanized. Another female broke a horn during the capture, but appeared in good condition on follow up monitoring. All collared animals were monitored daily for a period of 2 weeks. No other mortality or injuries were attributed to the capturing operation. In addition to helicopter net-gun captures, 2 bighorn sheep were darted on Mount Washburn in September. Carfentanil was used which required a park medic and veterinarian.

Blood taken during capture operations was tested for 17 diseases and parasites (Table 1). In addition, nasal swabs were tested for viral and bacteriological pathogens. Fifteen of these nasal swabs were negative for (*Pasturella* sp.). Two swabs had (*Pasturella hemolytica*) suspects isolated.

Table 1. Results of antibody reactions for 18 captured bighorn sheep from the Everts winter range.

SEROLOGICAL TESTS	#POSITIVE/#NEGATIVE	%POSITIVE
<i>Brucella abortus</i>	0/18	0.0
Blue Tongue	0/18	0.0
<i>Brucella ovis</i>	0/18	0.0
Infectious Bovine Rhinotracheitis	0/18	0.0
Bovine Virus Diarrhea	0/18	0.0
Bovine Viral Diarrhea Type II	0/18	0.0
Para Influenza-3	12/6	66.7
Leptospirosis 8 Serovars	1/17	5.6
Bovine Respiratory Syncytial Virus	16/2	88.9
Ovine Progressive Pneumonia	0/18	0.0

Samples were prepared and examined at the Veterinary Diagnostic Lab, Montana State University.

Movements

During the summer all collared bighorns were located at least 2-3 times a month. In the winter they were more accessible and could be located with greater frequency. A total of 1,019 group locations were made during the course of 18 months of fieldwork. Average group size for ewes was 10.08 (SD = ± 6.04) and for rams was 8.34 (SD = ± 5.14). These locations provided information on lambing sites, migration routes, watering areas, and areas with the potential for conflict with human activities (Fig. 5).

Three groups of ewes use the EWR and migrate to distinctly separate summer lambing ranges. Another ewe group (Deckard Flats) was in close proximity but was never documented south of the Yellowstone River. Ram groups did cross the river, spending time with this female group and linking all these groups genetically. Rams were both migratory, moving over 30-km southwest into the Gallatin Mountains, and resident around Mount Everts and McMinn Bench. The Mount Washburn group made the only complete migration of approximately 45-km. Lambing locations were located on cliffs above the eastside of the Yellowstone River. The McMinn group lambled on the east-facing cliffs of Sepulcher Mountain and made return trips to the winter range during the summer. The Rattlesnake Butte group was semi-resident on the winter range, after lambing in the Black Canyon of the Yellowstone River. They were never documented north of the Yellowstone River or east of Geode Creek. The Deckard Flats group lambled near Bear Creek in 1997 (north of the Park boundary) and farther up the Black Canyon in 1998 (within the Park boundary).

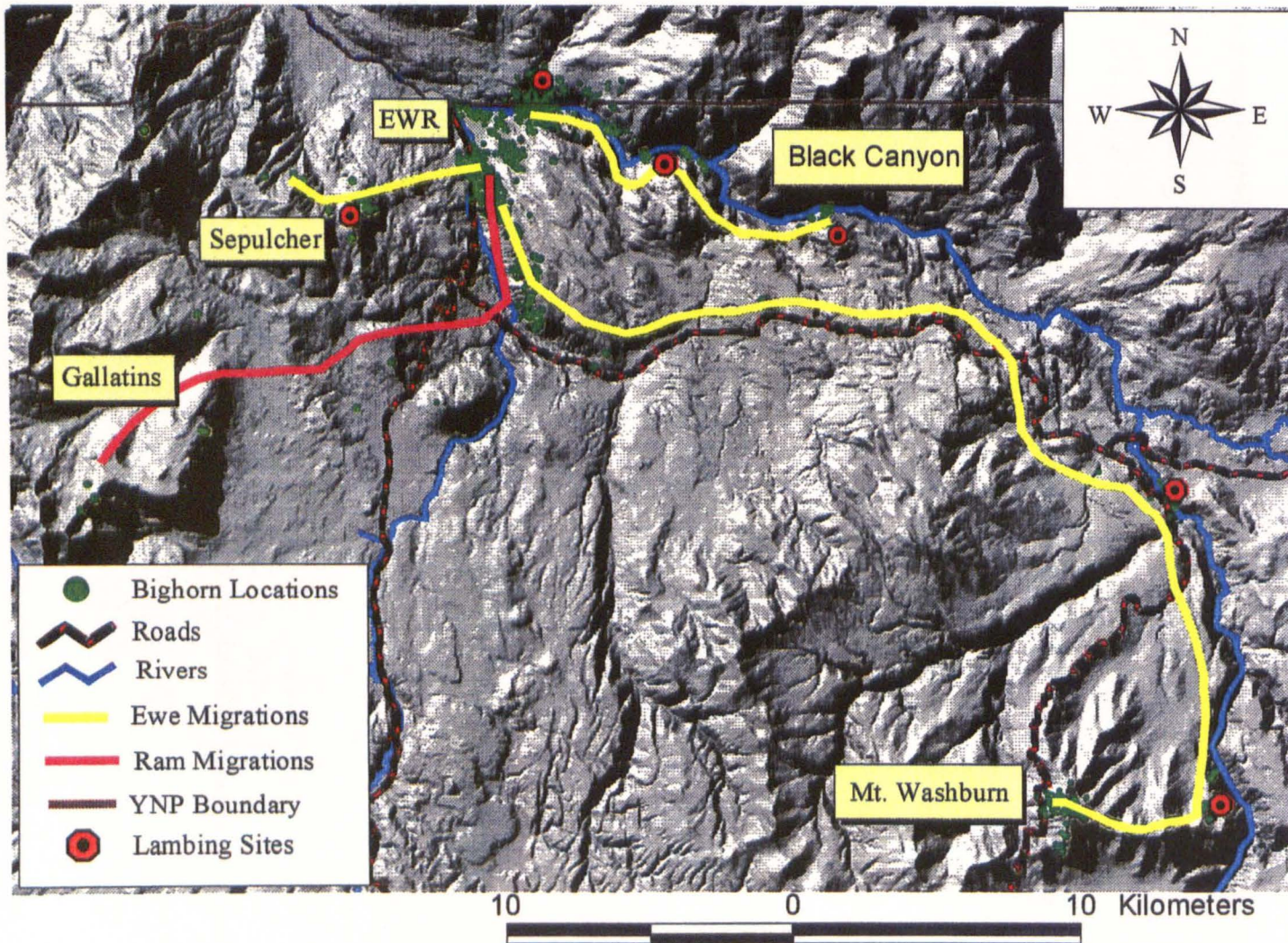


Figure 5. Migration routes of ewes and rams from the Mount Everts winter range.

Home ranges were calculated by season for the different groups of ewes and rams (Table 2). Winter ranges were significantly smaller for all groups except the Deckard Flats group that made early September moves to their winter range. Rams had larger home ranges during the summer than the females. This was partially an effect of the calculations that considered all rams as a single unit (a false assumption necessitated by few collared rams). One yearling ram (# 708), collared in the fall of 1997 on Mount Washburn, spent the summer of 1998 travelling repeatedly between Mount Washburn and McMinn bench. This ram was later located on Electric Peak and farther north (beyond the Park boundary) near Yankee Jim Canyon and traveled over 450 km during the summer (Fig. 5). The longest recorded migration was by ewes going 50 km to Mount Washburn (3,300 m) and rams going 25 km southwest into the Gallatins on Quadrant Mountain and Bannock Peak (3,000 m).

Table 2. Differences in home ranges between groups of bighorn sheep and their respective summer and winter ranges, calculated by the adaptive kernel method (95%).

GROUP	SUMMER ha. / # LOCATIONS	WINTER ha. / # LOCATIONS
McMinn	1,809 / 118	247 / 82
Rattlesnake B.	3,579 / 204	311 / 115
Mount Washburn	4,001 / 77	200 / 35
Deckard Flats	2,799 / 43	2,301 / 32
Rams	12,680 / 112	1,398 / 101

Population Status

Of 18 bighorn sheep collared in 1997, two collared females died. One death was due to mountain lion predation and the other old age (severe malnutrition in the spring). In addition to collared animal mortality, 6 other bighorns are known to have died in the EWR area. Two ewes died during the winter of 1997 due to severe abscesses in the lower jaw; 2 Class 4 rams apparently starved to death in the spring; a yearling female was struck by a car near La Duke Springs; and a ewe was crushed by a large falling rock.

The level of habituation and accessibility of the EWR bighorn sheep allowed a total count of 60 adults. In 1996-1997 I estimated that 32 adult ewes, 2 yearling ewes, 20 adult rams, 6 yearling rams and 3 lambs were associated with the EWR (9:100 lamb/ewe, December 1996). Most ewes produced lambs in 1997, but lamb mortality quickly occurred during early summer. By August the semi-migratory groups had no lamb survival, while the migratory group on Mount Washburn still had lambs. When the Mount Washburn group returned to the winter range, they immediately lost 2 more lambs (6:100 lamb/ewe, November 1997). The summer of 1998 resulted in one of the highest lamb production years (52:100 lamb/ewe, November 1998).

Nursing bout times are often used as a method of indicating forage quality and the health of the individual ewe (Shackleton 1973, Keating 1982, Haas 1990). In 1997 the average nursing bout was $(12.53 \pm 4.82, n = 15)$ and in 1998 $(16.47 \pm 9.17, n = 34)$. Average age of lambs observed nursing varies greatly between the 2 years and prevents comparisons.

Disturbances

The most obvious disturbances observed near the EWR were helicopter flights, motorized vehicles, humans on foot and predators. Coyote howling surveys were conducted during the spring of 1998 to determine pack densities around the winter range (4 packs of 2-3 individuals were estimated). During behavioral observations 1 predation attempt was noted by a golden eagle, 4 by packs of coyotes, and 1 by a mountain lion. Documented kills were recorded for 2 adult ewes killed by lions. A lion study beginning in 1998 found an adult lion with 2 kittens frequenting the EWR area.

The number of observations associated with human presence (determined as visible or audible to bighorn sheep) was recorded. Disturbances to bighorn sheep during these observations were determined from behavioral activity ranging from alert postures, nervous walking and grazing activity, and flight away from the area. Since the bighorn sheep in YNP are habituated to humans, most recreational activity does not cause noticeable disturbances. This was especially true on Mount Washburn where over 50 % of the observations took place with humans in the vicinity, and only about 8 % of the observations with human presence caused an overt disturbance (Table 3).

Different groups were exposed to different types of human activities that cause greater or lesser disturbance reactions in bighorn sheep. Most of the human presence on Mount Washburn was on foot and was less disturbing than other types of human activities. The Rattlesnake Butte group received the lowest overall disturbance rate of 2.9 %, with 71.4 % of these disturbances related to aircraft. Since this group is rarely near a road or hiking trail, the chance for disturbances from humans on foot or in vehicles

is very low. The McMinn bench group spent more time near the Gardiner-Mammoth road and was more visible and accessible to hikers and photographers, thus receiving greater disturbances from road traffic and humans on foot. In addition, the McMinn bench group received the highest number of disturbances related to air traffic. Air traffic caused the greatest and most consistent disturbances to bighorn sheep in all groups (accounting for 36.1 % of all disturbances). Combined disturbance types for the McMinn bench group resulted in the highest overall disturbance rate of 7.5 %.

Table 3. Human related disturbances of bighorn sheep groups during 10-min behavioral observations.

	GROUPS				
	McMinn	Rattlesnake	Deckard	Rams	Washburn
Total observations	146	240	74	197	117
Observations with human presence	53 (36.3 %)	28 (11.7 %)	11 (14.9 %)	33 (16.8 %)	60 (51.2 %)
Human presence resulting in disturbances	11 (20.8 %)	7 (25.0 %)	4 (45.5 %)	9 (27.3 %)	5 (8.3 %)
Disturbances related to aircraft	6	5	1	1	0
Total disturbance rate	7.5 %	2.9 %	5.4 %	4.6 %	4.3 %

Helicopter flights occurred primarily between June and September and were concentrated around the EWR due to local topography and the heliports in Gardiner and Mammoth. Helicopters caused greater disturbances than fixed-wing aircraft. The total number of contract flights out of the Mammoth heliport during 1995 and 1997 were 170 and 175 flights, respectively. During 1997-1998 an increase in helicopter flight activity

occurred during the winter months, primarily related to wildlife research within YNP. Of the 8 helicopter flights that were witnessed during behavioral observations, only 1 did not elicit a disturbed response. Disturbances occurred at distances over 2.5 km and even when the helicopter was not visible to bighorn sheep. On several occasions helicopter flights over the EWR during the winter caused sheep to run up to 250 m and even abandon wind blown slopes at lower elevations for up to one week.

Vehicle Traffic

Vehicle traffic in YNP has almost doubled in the past 10 years. Between June and September traffic flow on Dunraven Pass averages 4,022 vehicles per day. Hourly traffic flow patterns peak at 400+ vehicles per hour between 1400 and 1600 hrs (Fig. 6).

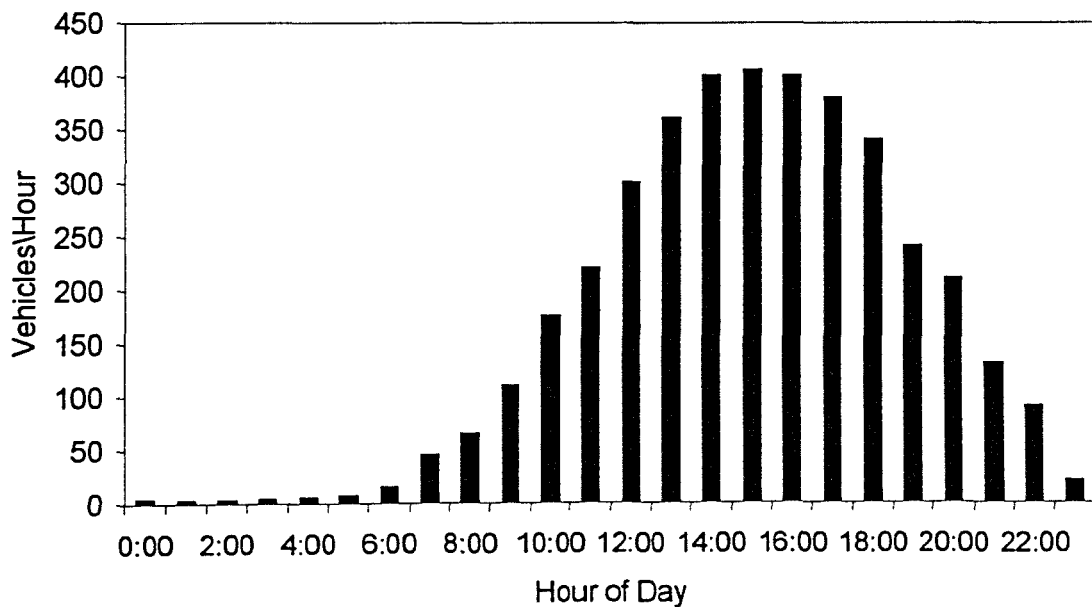


Figure 6. Hourly traffic flow patterns on Dunraven Pass between June and September. Compiled from Transportation Study of Dunraven Road (1997, NPS Report).

The Gardner-Mammoth road is maintained year-round. Average daily traffic flows during the winter and summer months of 1997 and 1998 were 1,205 and 3,764, respectively (Fig. 7). There is basically a continuous flow of traffic during the summer and intermittent traffic flow during the winter. The average hourly traffic (AHT) remains elevated above 250 between the hours of 800 and 1600 during the summer. There are noticeable increases in vehicle traffic during the hours of 700 and 1600 and 1700, presumably from employees going to and from work in Mammoth (Fig. 8).

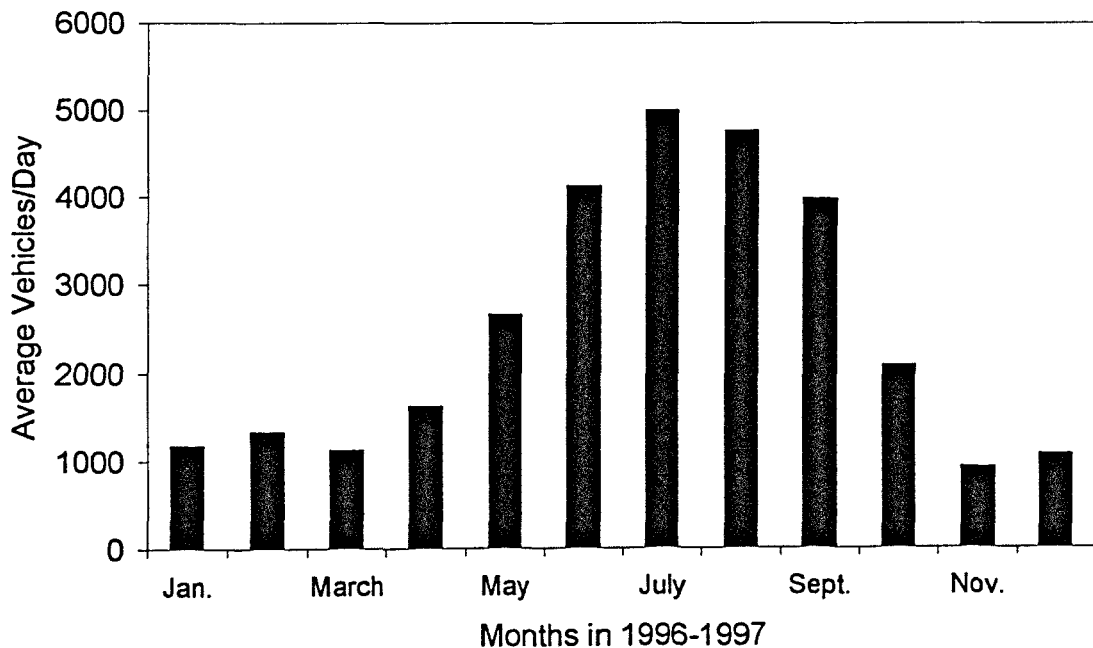


Figure 7. Average daily vehicle flow on the Gardiner-Mammoth road by month.

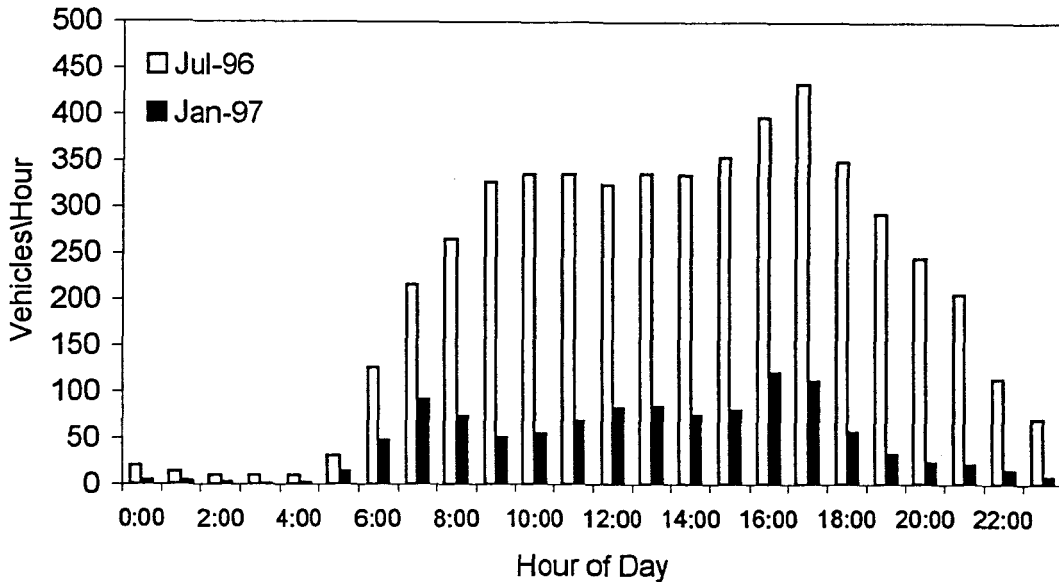


Figure 8. Hourly vehicle flow on the Gardiner-Mammoth road using July and January as representative months for summer and winter.

Road Corridors through the EWR

Both ewes and rams use the Gardiner-Mammoth road corridor during the summer and winter months. Approximately 32.9% ($n = 123$, Total bighorns = 1,082) of all group observations taken on the EWR occurred within the 150-m buffer of the Gardiner-Mammoth highway. The rest of the observations (approximately 65%) occurred above the canyon on McMinn bench and Mount Everts. Seeps located along the cliff face provide water and possibly minerals during the summer. All watering locations along the Gardner River occurred at locations where sheep could access the river without crossing the road (Fig. 9). Ewes, which lambled on Sepulcher, crossed the canyon on the bridge near Eagle Nest rock in late May or early June. At this time, when traffic is low and

there are no lambs, the road did not cause as much disturbance. During the summer of 1997 and 1998 ewes with lambs returned to McMinn bench in late June and early July. Observations identified potential problems with increased traffic volume (5,000 vehicles per day) during this time of year. Bighorn sheep with lambs acted agitated and nervous when approaching the road. During some crossing attempts, sheep retreated from the road and returned several times before finally crossing when traffic stopped.

Using a 150-m buffer zone (Smith et al. 1991) the number of group observations occurring within the proposed road buffer were calculated (23.8 %, $n = 77$, total bighorns = 988). The Old Gardiner-Mammoth road only had 1.2 % ($n = 4$, total bighorns = 36) of all observations made on the EWR (Fig. 10).

Dunraven Pass Road Corridor

The Mount Washburn group had 13.7 % ($n = 11$, Total bighorns = 143) of all group observations occurring within the 150-m road buffer. Most road observations were associated with begging behavior along a $\frac{3}{4}$ -km section of road in the late afternoon, primarily in August or September. During the fall migration the Mount Washburn ewes spent about 1–2 weeks near Tower Falls in late October where they grazed and moved along the road, which was closed to vehicles at that time. The migration route went behind the Tower ranger station through the Lost Lake area to Phantom Lake, where they spent a few days and then moved back to McMinn bench by the first week of November (Fig. 5). A separate, small group of sheep occupied the cliffs east of Calcite Springs across the Yellowstone River.

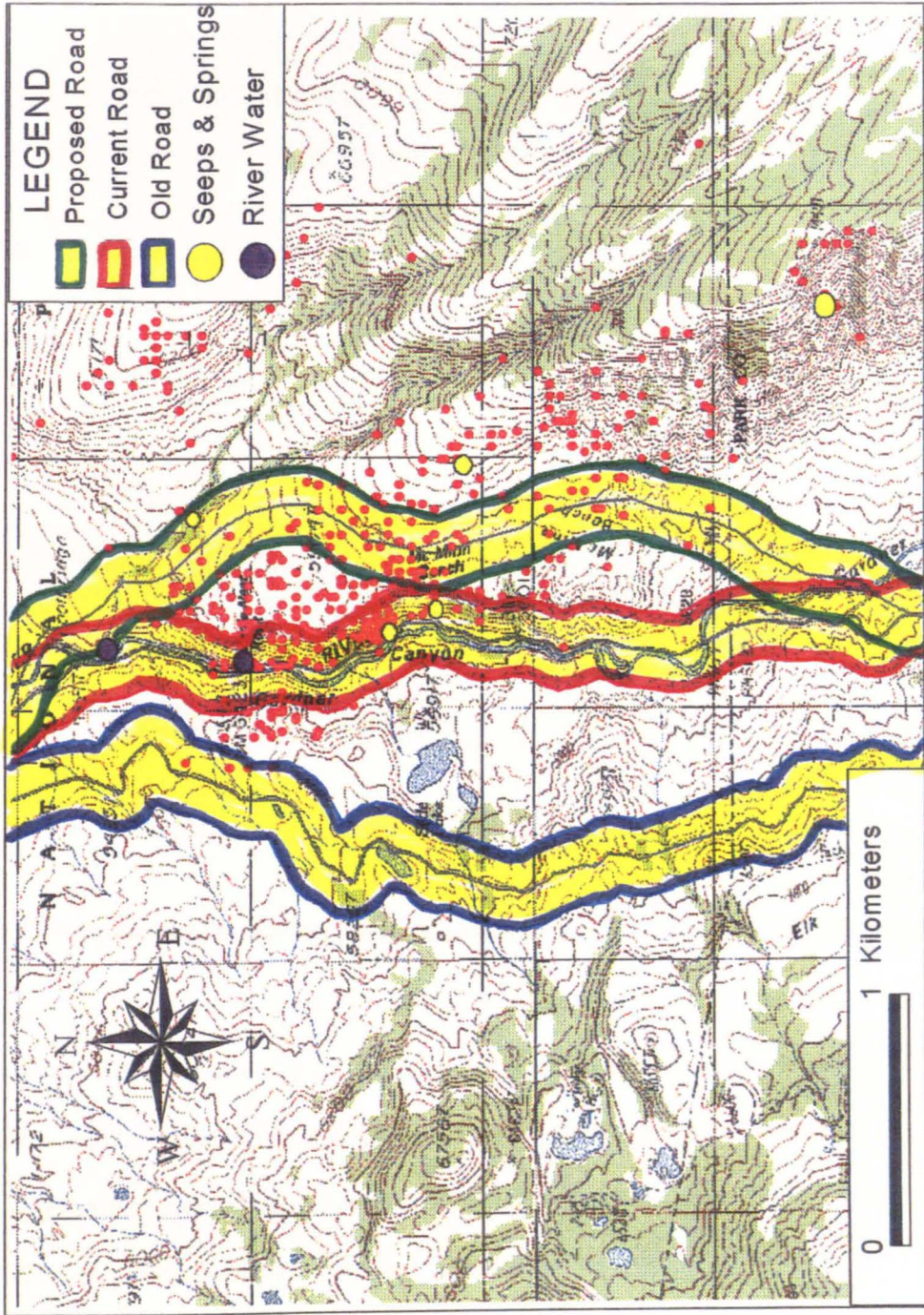


Figure 9. The Gardiner-Mammoth road corridors in relation to watering sites and all group locations of bighorn sheep.

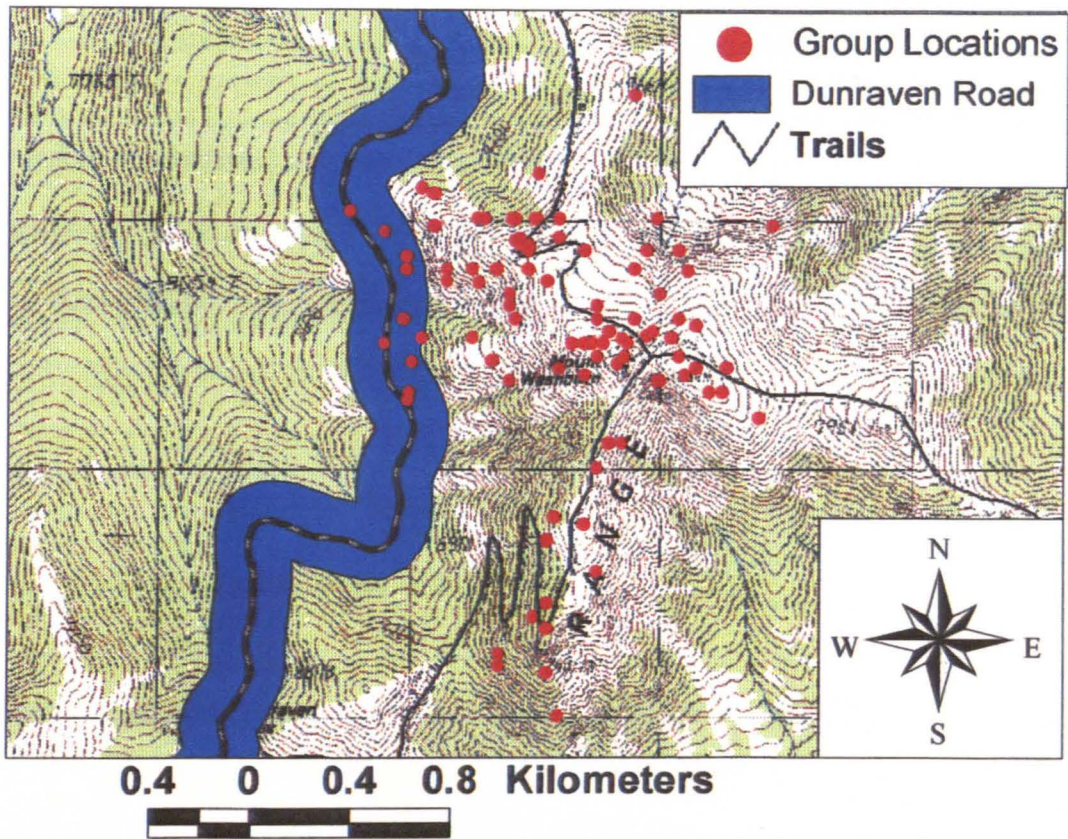


Figure 10. Group locations of bighorn sheep on Mount Washburn and their relation to hiking trails and the 150-m buffer on the current road corridor.

In addition to the vehicle traffic over Dunraven Pass, there is considerable foot traffic up to the top of Mount Washburn from two separate parking areas. During the summer months up to 100 visitors a day can reach the peak. Buffer zones of 50 m were applied to the trails because disturbance from humans on foot was not as great or as frequent as from roads. A total of 23 observations fell within the trail buffer zones (29 % of all observations) on Mount Washburn.

Behavior

A total of 762 observations were used for the analysis. The behavioral data were initially classified into 5 categories (Fig. 11). The level of activity was used to examine differences among groups subject to different disturbance levels from humans. All behavioral data were pooled and classed into active and inactive categories, with activity used as the dependent variable in all tests ($\bar{x} = 0.628$, CI 95% = ± 0.028 , $n = 762$). PROC-MIXED was used with date and individual sampled set as random variables. Repeated measures of individuals did not have a statistically significant impact on the analyses of the data (REML Covariance parameter estimate < 0.001 versus overall residual = 0.459). The date did have a minor effect (REML = 0.005).

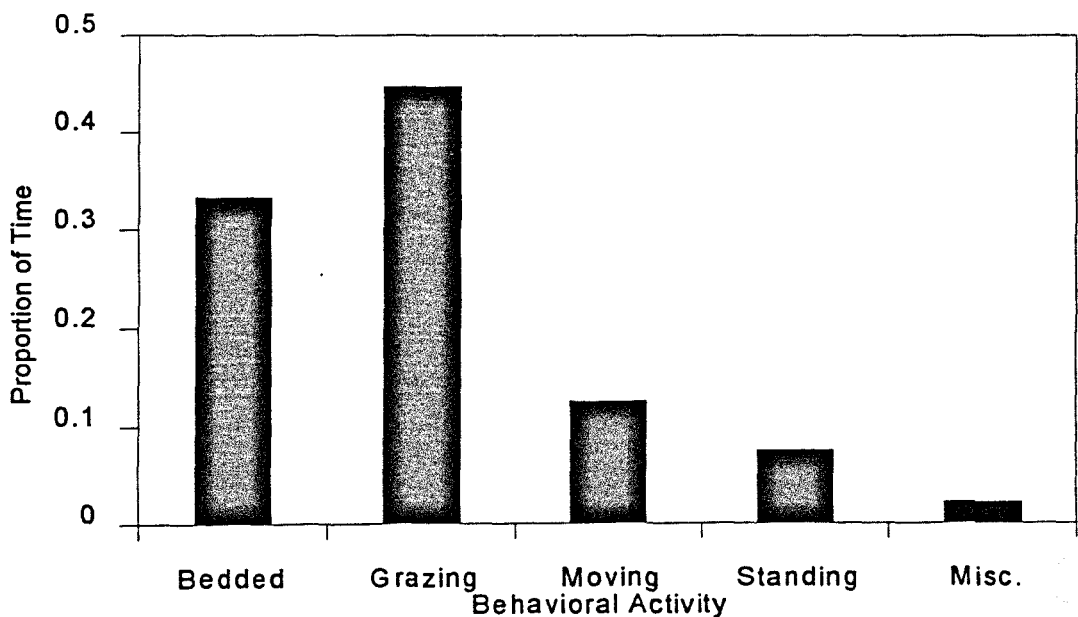


Figure 11. Mean behavioral activity combined for all groups of bighorn sheep.

The PROC-MIXED analysis identified statistical differences in activity at the 95 % confidence level for season (DF = 428, $F = 8.45$, $P < 0.001$) and time of day (DF = 428, $F = 7.00$, $P = 0.001$). Differences in overall group activity levels were not found (DF = 428, $F = 1.85$, $P = 0.118$). Differences were examined among Class 1 & 2 rams (< 3 years old) versus ewes, ewes versus mature rams (Class 3 & 4), young rams versus mature rams, migratory ewe groups versus non-migratory, McMinn bench and Mount Washburn, Rattlesnake Butte and Mount Washburn and McMinn bench and Rattlesnake Butte. The only significant differences found among groups was between McMinn bench and Rattlesnake Butte (DF = 428, $F = 5.48$, $P = 0.020$).

Seasonal differences exist in activity levels between summer and winter (DF = 428, $F = 8.90$, $P = 0.003$) and summers (DF = 428, $F = 5.06$, $P = 0.025$) (Fig. 12).

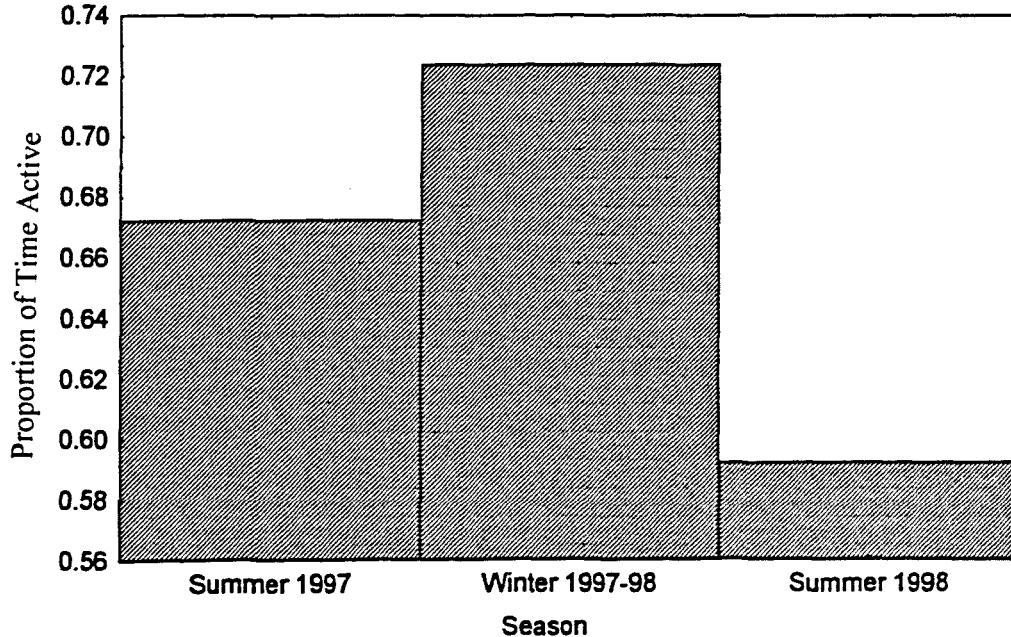


Figure 12. Seasonal differences in mean activity levels among all bighorn sheep groups and time periods.

Bighorn sheep were more active during evening hours than in the morning or afternoon periods (DF = 428, F= 12.88, $P < 0.001$) and afternoon hours (DF = 428, F = 9.43, $P = 0.002$). There was no significant difference between morning and afternoon activity levels (Fig. 13).

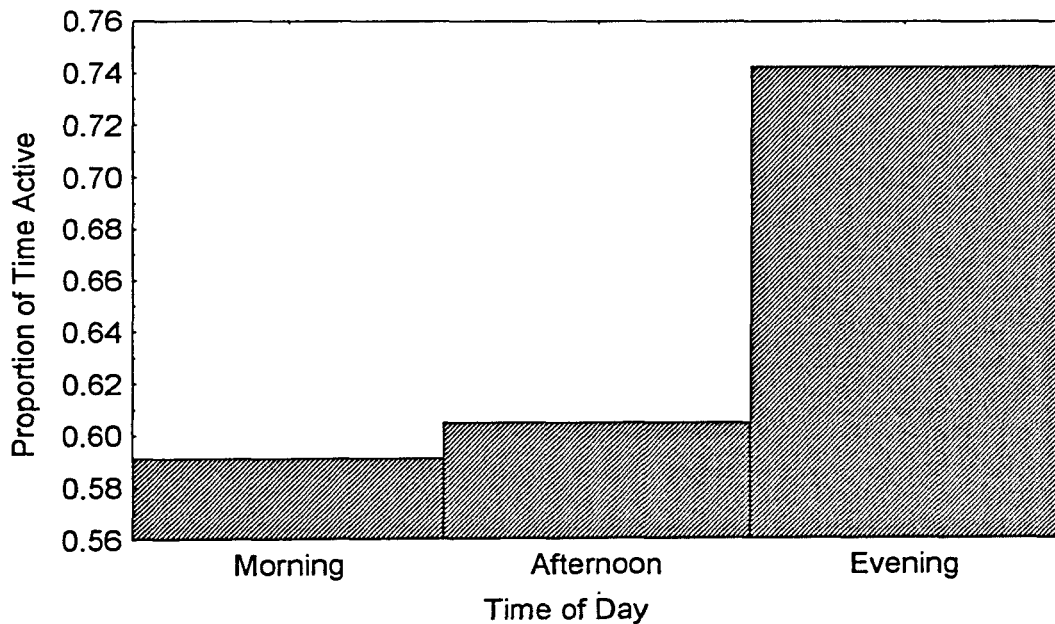


Figure 13. Diurnal differences in mean activity levels among all seasons and groups of bighorn sheep.

Lungworm Analysis

A total of 372 fecal samples were collected over 12 months. Initial comparisons revealed a striking disparity in the sensitivity of the Baermann versus the beaker tests. False negatives were found in the Baermann tests ($n = 21$) as well as a high number of very low counts (< 2) of lungworm larvae (Baermann = 74, Beaker = 40). Prevalence

of *Protostrongylus* infection in known individuals was 96 % ($n = 25$) in both tests. There was only one individual (# 671) in the group that always tested negative.

To compare with other studies where samples are collected from unknown individuals, the prevalence of positive samples was calculated. The beaker technique revealed a 90 % infection rate and the Baermann method only 85 %. The beaker technique resulted in much higher levels of LPG than the Baermann method. Mean \pm SE beaker and Baermann LPG results for rams = 284 ± 40 , ewes = 476 ± 41 and rams = 74 ± 13 , ewes = 163 ± 16 , respectively. The highest LPG levels of the beaker technique were more than twice that of the Baermann method (beaker = 4,750, Baermann = 2,048). These data are presented only as a reference to compare with other studies (Fig. 14).

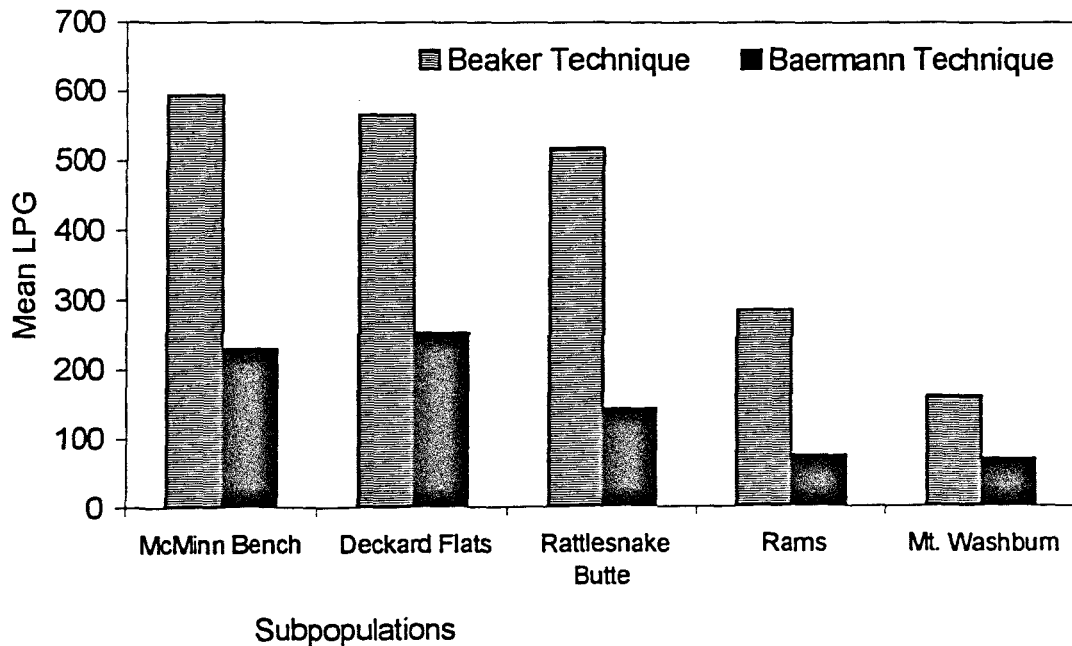


Figure 14. Mean larvae per gram of feces (not transformed values) among groups of bighorn sheep associated with the Everts winter range.

Utilizing samples from identifiable and collared animals allowed the tracking of monthly changes in LPG (values are not transformed) shedding in individuals among groups. Seasonal shifts in LPG shedding were evident in all individuals except ewe 671, the only ewe that always tested negative. Ewe BLS was the only female that changed summer lambing areas from Mount Washburn in 1997 to McMinn Bench in 1998. While originally from the Mount Washburn group, she was classified with the McMinn group based on summer movements and associations with sheep from that group. (Fig. 15, 16, 17, 18).

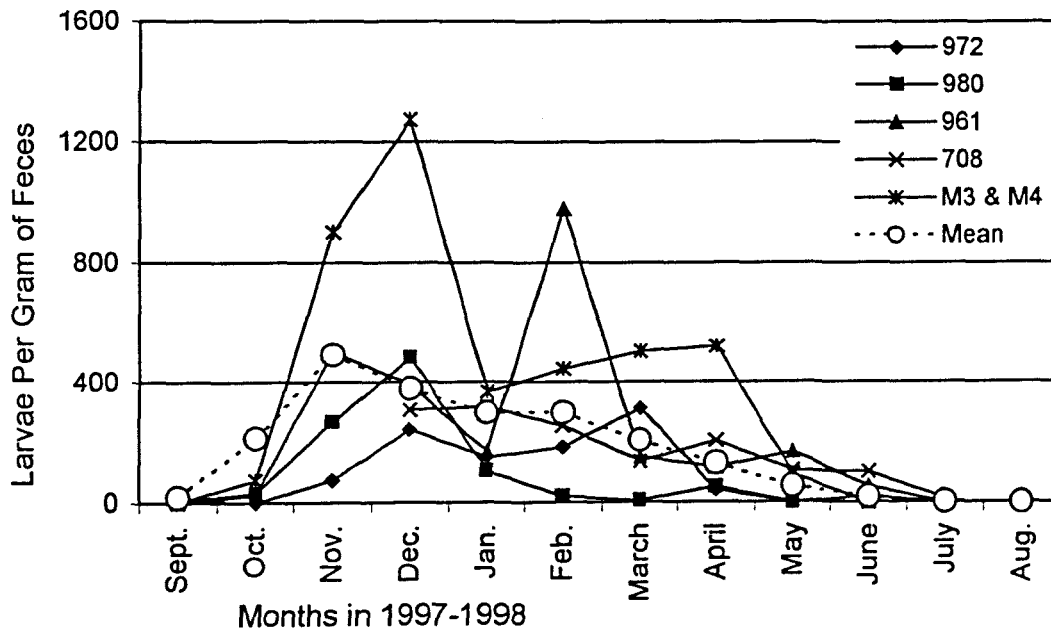


Figure 15. Monthly larvae per gram of feces (values are not transformed) from known individual bighorn rams.

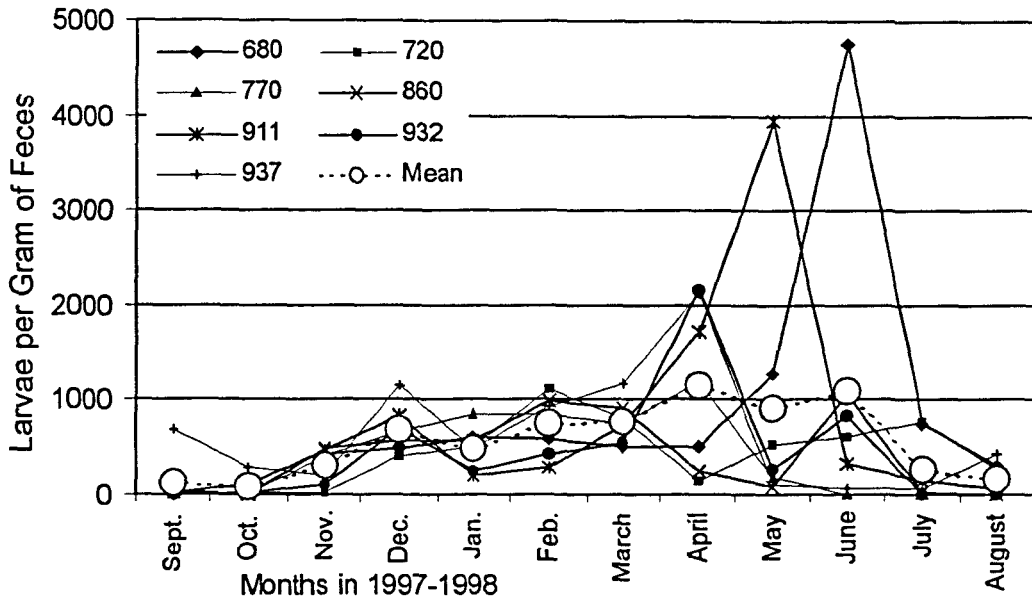


Figure 16. Monthly larvae per gram of feces (values are not transformed) from known individual bighorn sheep in the Rattlesnake Butte group.

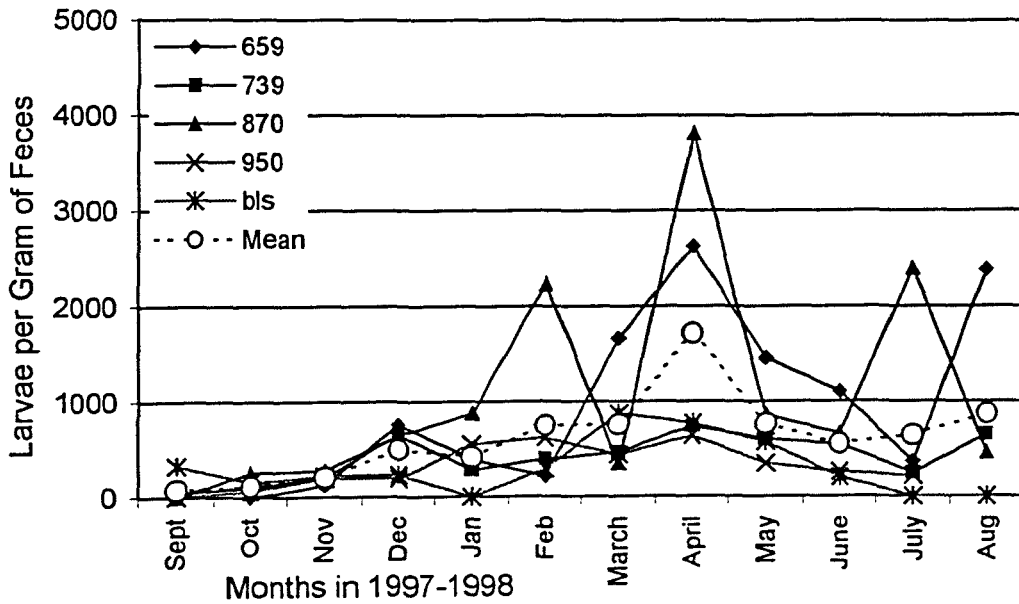


Figure 17. Monthly larvae per gram of feces (values are not transformed) from known individual bighorn sheep in the McMinn Bench group.

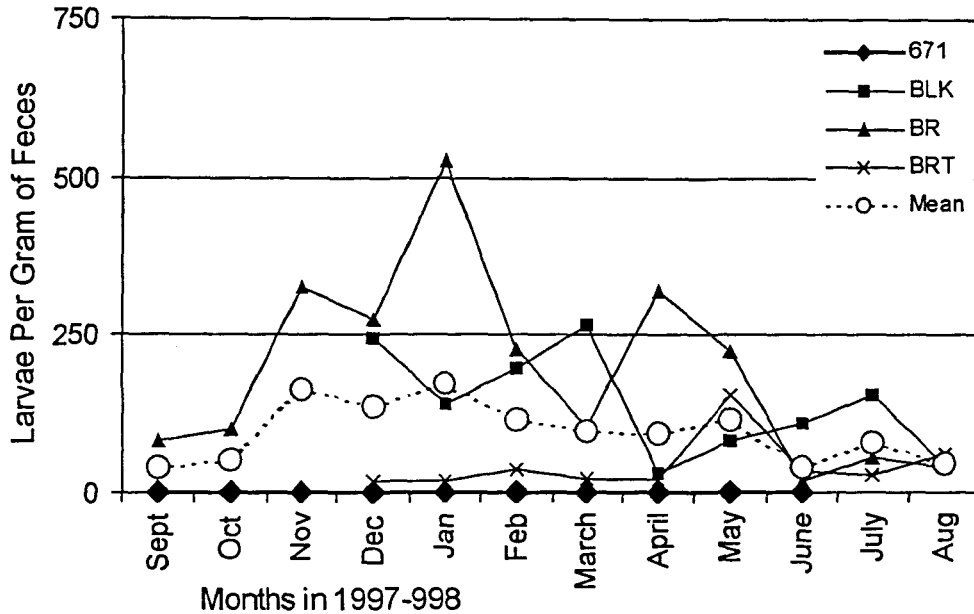


Figure 18. Monthly larvae per gram of feces (values are not transformed) from known individual bighorn sheep in the Mount Washburn group.

Cubed root transformations (tLPG) were used to normalize the distribution of data. There was a strong correlation between the tLPG in the two techniques ($r = 0.755$, $P < 0.001$, $n = 372$). All other analyses were conducted using transformed (tLPG) from the more sensitive beaker method. The PROC-MIXED program was used to test for differences among groups, months and sexes, with individuals set as a random variable. The REML estimates for the model were 2.805 for individual and 5.823 residual, indicating that the repeated samples of individuals did not have a greater effect than overall residuals in the model. The effects of group were not statistically significant (DF = 326, $F = 2.04$, $P = 0.073$), but there were differences between sexes (DF = 326, $F = 4.76$, $P = 0.030$) (Fig. 19).

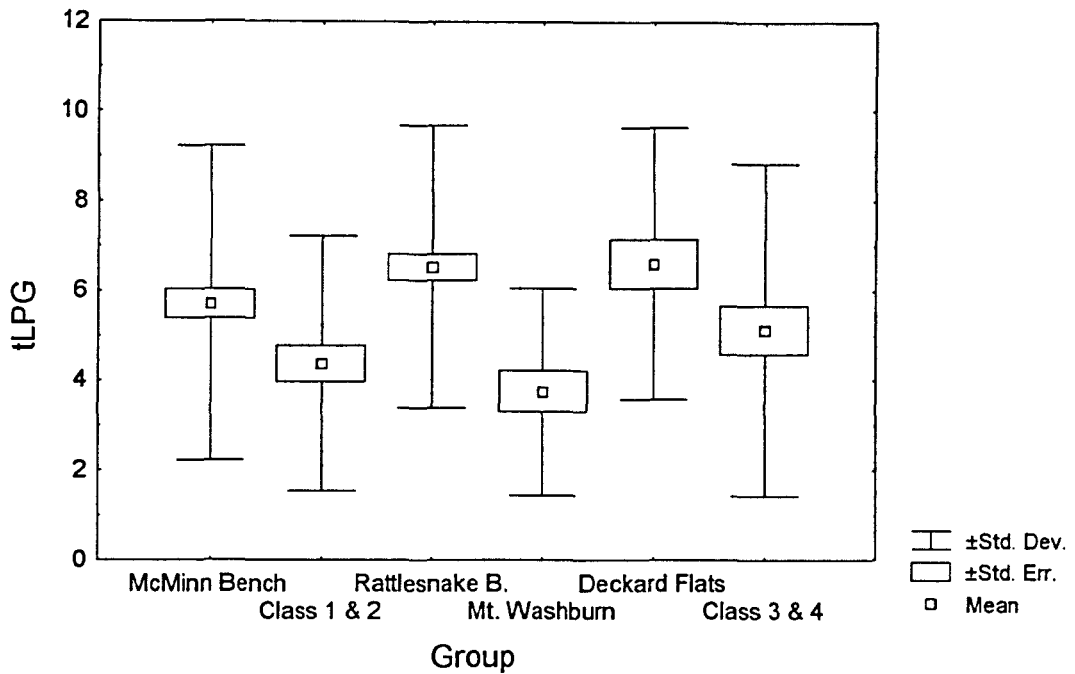


Figure 19. Differences in larvae per gram of feces (transformed values) from bighorn sheep groups associated with the Everts winter range

There was strong inter-month variation ($DF = 326$, $F = 16.38$, $P < 0.001$). The yearly mean tLPG for rams was lower than ewes, peaking in December 1997, and steadily declining to nearly 0 by August 1998. Ewe tLPG levels increased through fall and winter (October - March) 1997 and remained elevated during the summer (April - September) of 1998. Ewe shedding rates were more variable than male shedding rates throughout the spring and summer (Fig. 20).

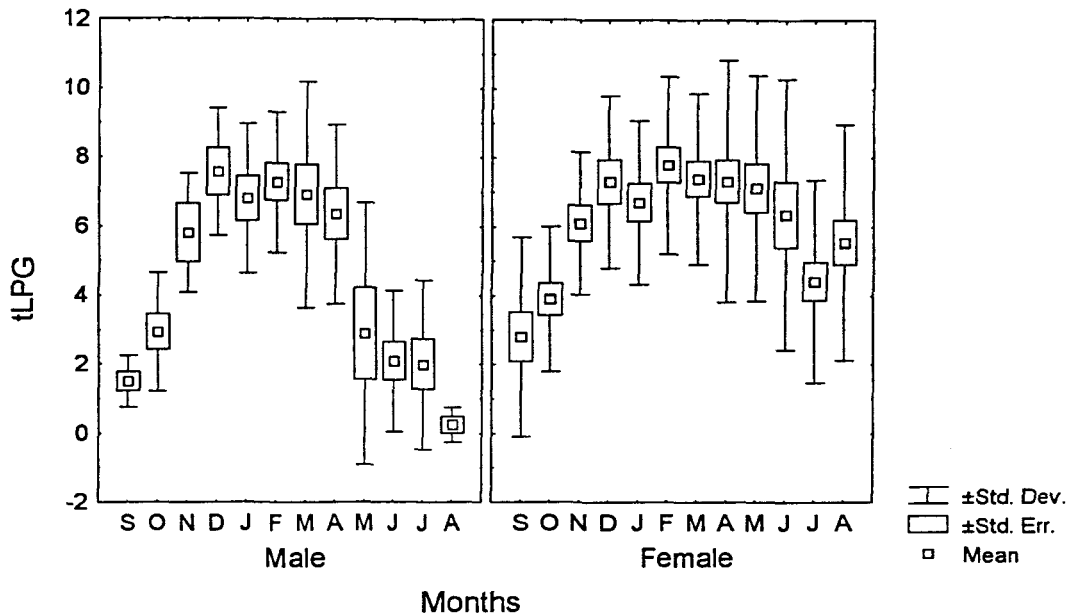


Figure 20. Yearly cycle of larvae per gram of feces (transformed values) in rams and ewes associated with the Everts winter range.

Post hoc tests revealed significant differences in tLPG between the McMinn bench group and Rattlesnake Butte group ($Df = 326$, $F = 7.24$, $P = 0.008$). No statistical differences were found between the Mount Washburn group and other ewe groups. Differences were found between summer and winter months for rams ($DF = 96$, $F = 120.5$, $P < 0.001$) and ewes ($DF = 224$, $F = 50.88$, $P < 0.001$).

The age of the sheep and level of tLPG in rams and ewes were examined. Ewe ages were limited to collared animals (average age = 6 yrs). Regression analysis for ewes revealed a negative correlation ($r = - .5185$, $P = 0.102$, $n = 13$). Without ewe 671, who was old and negative for lungworm, the regression was still negative ($r = - 0.166$). The regression for the rams was positive ($r = 0.729$, $P = 0.100$, $n = 6$).

Corticosterone Levels

A total of 384 samples were assayed for levels of corticosterone. A regression of paired samples of corticosterone and lungworm levels had no correlation ($r = 0.024$, $P = 0.665$, $n = 332$). PROC-MIXED REML estimates satisfactorily handled repeated samples of individuals (individual residual = 0.002, overall model residual = 0.027).

Significant differences were found among groups (DF = 318, $F = 2.28$, $P = 0.046$), months (DF = 318, $F = 11.58$, $P < 0.001$) and sex (DF = 318, $F = 4.56$, $P = 0.033$) but not between collared and uncollared sheep (DF = 318, $F = 0.760$, $P = 0.384$) (Fig. 21). No differences were found in old versus young males (DF = 318, $F = 0.190$, $P = 0.665$) or young males versus females (DF = 318, $F = 2.63$, $P = 0.106$) (Fig. 22).

Differences in corticosterone levels in migratory versus non-migratory ewes (DF = 318, $F = 0.870$, $P = 0.351$) were also insignificant. Non-migratory groups in similar habitats were compared based on human disturbance level. The McMinn Bench group, which had higher levels of human disturbance, had higher levels of corticosterone than the less frequently disturbed Rattlesnake Butte group (DF = 318, $F = 6.31$, $P = 0.013$). Deckard Flats and Rattlesnake Butte were also compared and were not found to be significantly different at the 95% level (DF = 318, $F = 3.69$, $P = 0.056$). The same insignificant results were found when comparing corticosterone levels from McMinn Bench to those of Deckard Flats (DF = 318, $F = 3.69$, $P = 0.056$) (Fig. 23). Since the P -values in the previous two tests approached significance, the correlation between corticosterone and disturbance levels in each pair-wise test was examined. The greater disturbance levels did correspond to the higher level of corticosterone in each group.

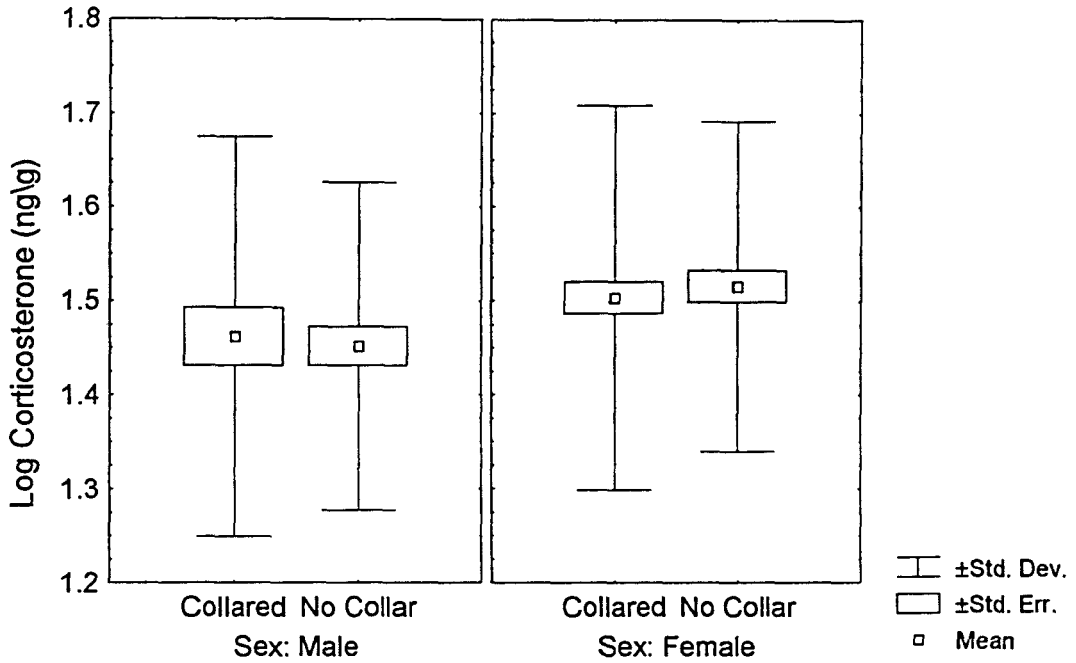


Figure 21. Similar levels of corticosterone found in radio collared and uncollared bighorn sheep associated with the Everts winter range.

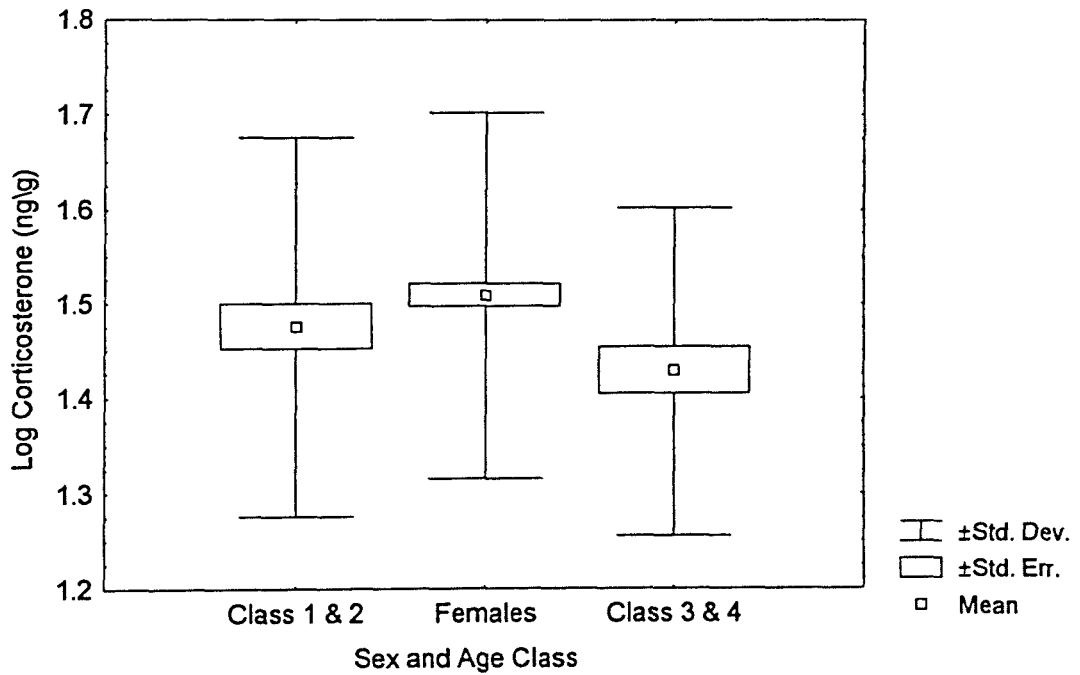


Figure 22. Differences in the corticosterone levels between age classes of rams (Class 1 & 2 < 3 years old, Class 3 & 4 > 3 years old) and all ewe groups combined.

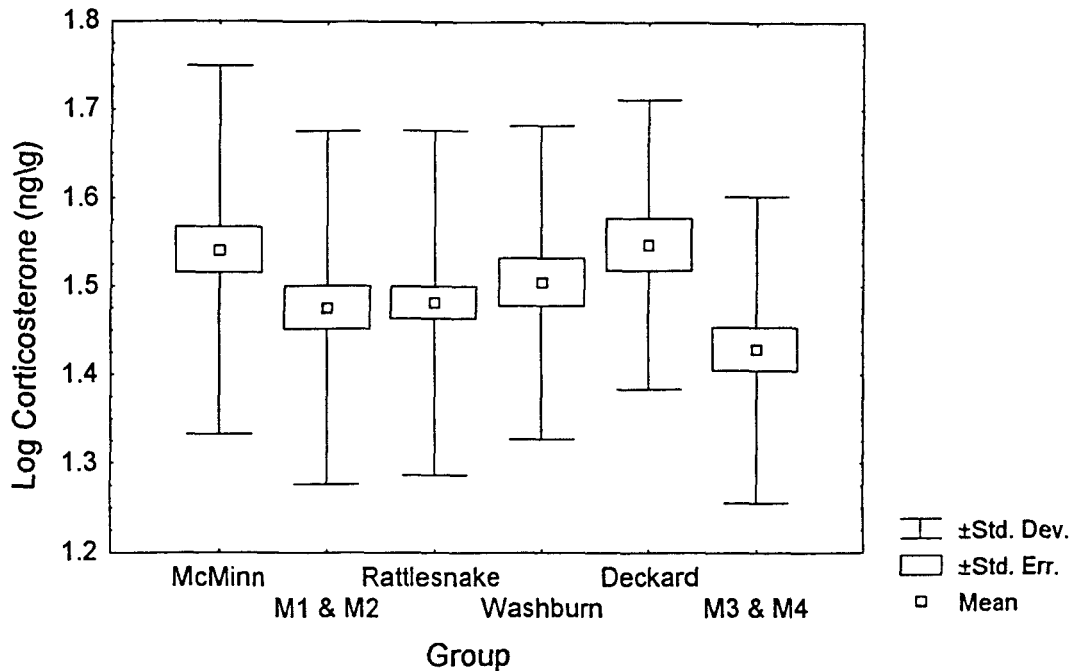


Figure 23. Yearly corticosterone (ng/g) levels among ewe groups and age classes of bighorn sheep (M1 & M = males < 3 years old, M3 & M4 = males ages >3).

Corticosterone levels for all individuals varied by month (Fig. 25, 26, 27, 28).

Patterns were evident for season and among sex and age classes. Corticosterone levels in both rams and ewes declined throughout the winter months and then surged during the month of May. In ewes the spike in May (DF = 95, F = 65.5, $p < 0.001$) was significantly higher than all other months. Ram corticosterone levels during the winter (October – March) were significantly lower than summer (April – September) levels (DF = 95, F = 65.5, $p < 0.001$) (Fig. 24). Some lambs were sampled from ewe groups on Deckard Flats, Sepulcher Mountain and Mount Washburn during the summer of 1998. The average transformed corticosterone level for lambs was $(1.494 \pm 0.135, n = 11)$.

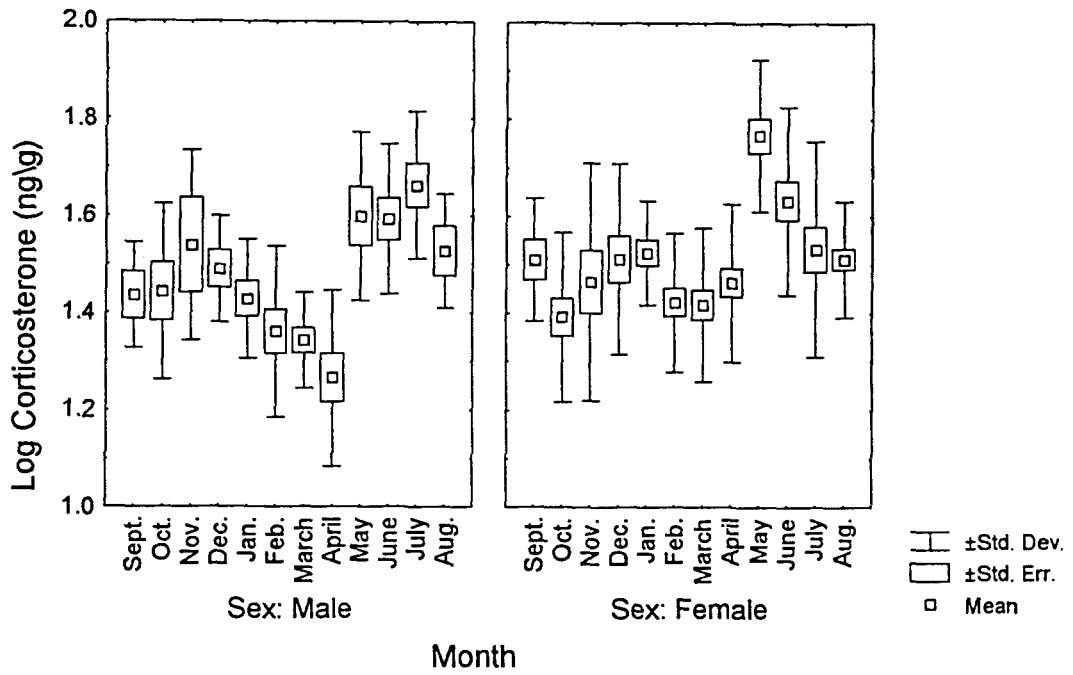


Figure 24. Yearly cycle of corticosterone (ng/g) in male and female bighorn sheep.

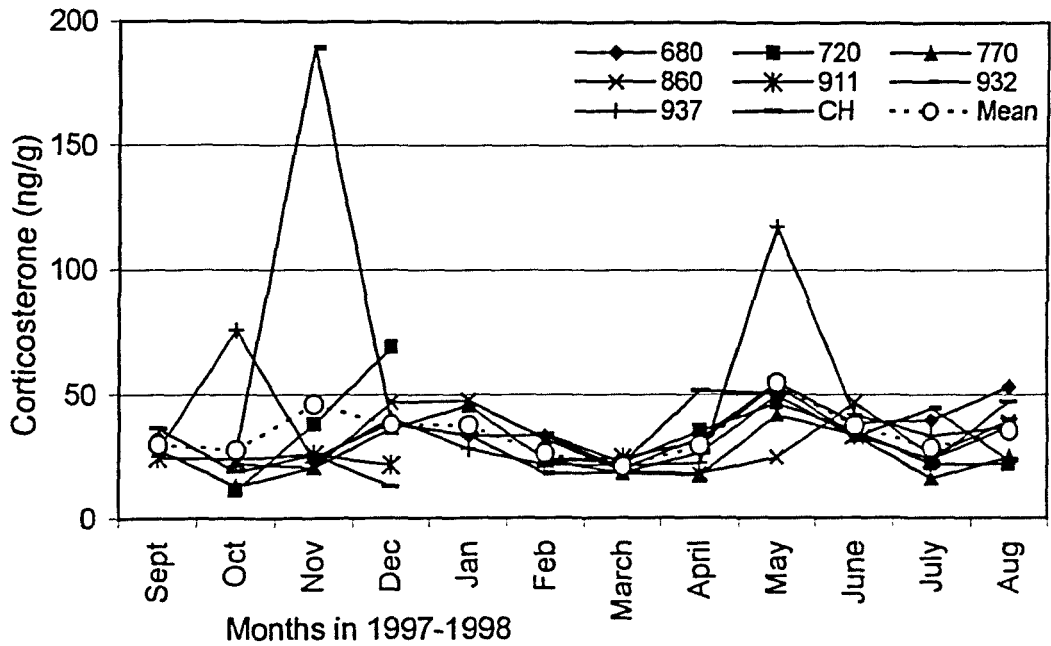


Figure 25. Corticosterone (ng/g) levels from ewes in the McMinn Bench group.

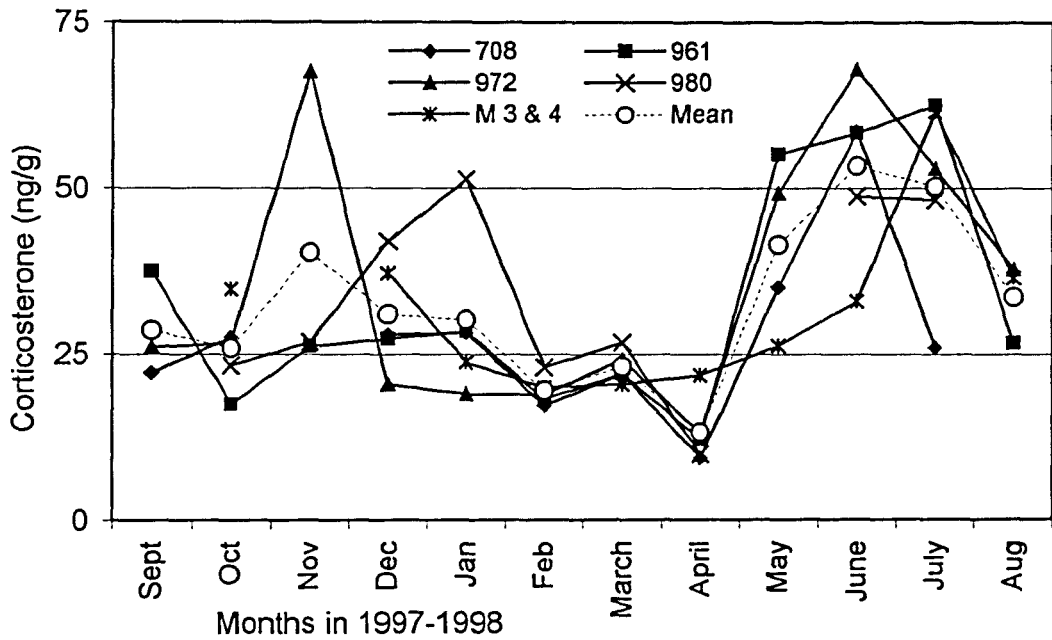


Figure 26. Corticosterone (ng/g) levels from collared rams (1-3 years) and Class 3 & 4 rams (>3 years) associated with the Everts winter range.

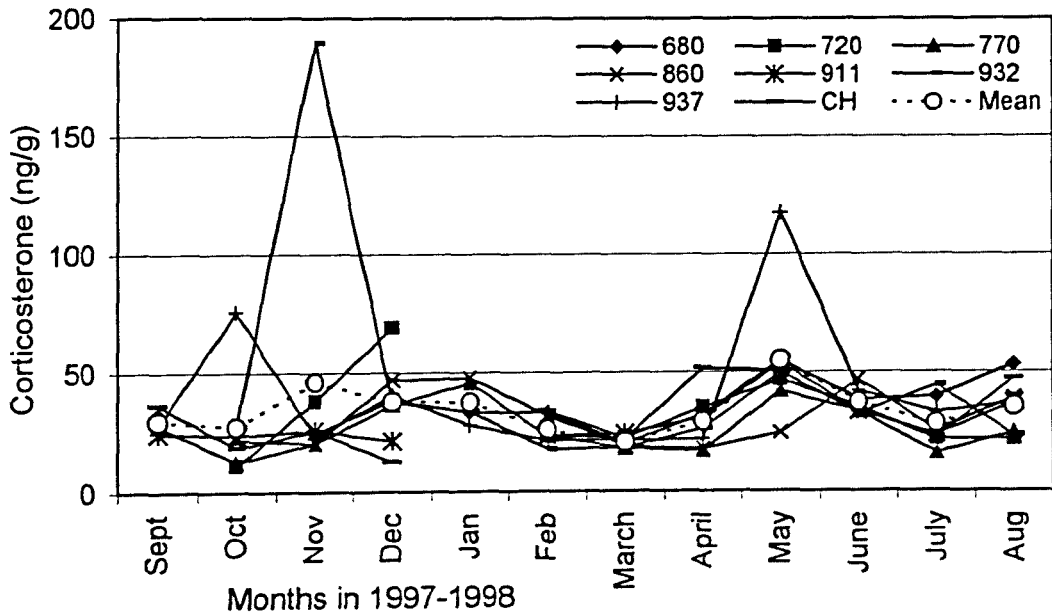


Figure 27. Corticosterone (ng/g) levels from ewes in the Rattlesnake Butte group.

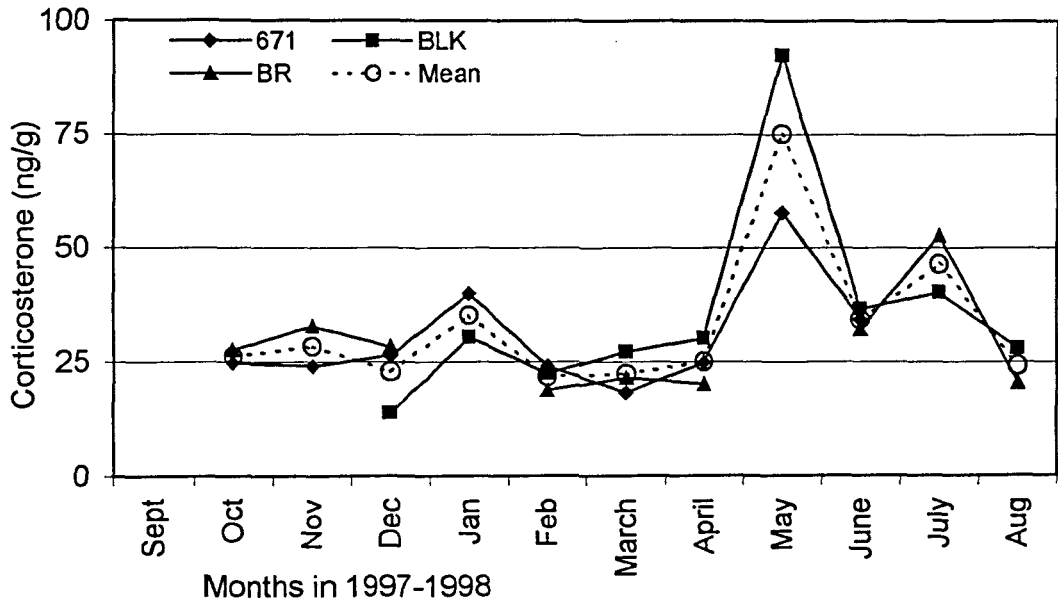


Figure 28. Corticosterone (ng/g) levels from identifiable ewes in the Mt. Washburn group.

DISCUSSION

Seasonal Movements and Disturbances near the EWR

Different migratory routes and strategies were observed in 4 distinct ewe groups and 2-3 ram groups associated with the EWR. Wildlife researchers often classify bighorn sheep according to a geographic winter range (Horejsi 1976, Festa-Bianchet 1986). Both rams and 3 of the ewe groups used the core area (McMinn Bench) of the EWR throughout the year

The Mount Washburn group used the area from November till late May, the Rattlesnake Butte for 2-3 weeks during the rut and spring green-up, and the McMinn Bench ewe group and ram groups during any month. The migratory or non-migratory nature of these groups may expose them to different climatic conditions, predator levels, interspecific competition, parasite loads and human activities (Wishart et al. 1980, Fryxell et al. 1988).

Watering sources and mineral licks are seasonally important and are located along the east cliff face within 15 m of the main road. In exceptionally dry years these sources may dry up forcing sheep to use the river (which is closer to the road) more frequently. All watering sites occurred in places where sheep did not have to cross the road to access the site. Guardrails, placed in the 1970's through parts of the canyon, may further limit bighorn sheep movements and access to some areas (Meagher pers. comm.). Use of natural structures for guardrails, such as stone or wood, may allow easier movements by bighorn sheep. I saw bighorns moving over and on both stone and log guardrails. Realignments of the current road west of the Gardner River could increase available

watering areas and winter habitat in places where the road may currently act as a barrier. Winter use of the riparian areas and lower cliff faces occurred primarily after heavy snows forced the sheep off the upper meadows.

The proposed road option over McMinn Bench would disturb 3-4 separate groups of bighorn sheep. More frequent road crossings by groups, seeking shelter, water or minerals in the cliffs would be expected. Only 33 % of all observations on the EWR occurred within the 150-m Gardner-Mammoth road buffer. The remainder of the observations (65 %) occurred on top of McMinn Bench 200-300 m away from the cliff face in the area of the proposed road.

Aircraft have been cited as one of the more disturbing human activities for bighorn sheep (Miller and Smith 1985). Aircraft traffic (both fixed-wing and helicopter) in YNP may be increasing and caused 36.1 % of all overt disturbances to bighorn sheep. Currently, research aircraft (primarily fixed wing) account for the majority of flight activity.

Bighorn sheep on the EWR may be fairly habituated to fixed-wing aircraft above certain elevations since they are in a primary flight corridor. During my aerial relocations, overt disturbance behavior was noted on numerous occasions. Levels of disturbances seem to be related to the altitude of the aircraft and the number of passes made over the bighorn sheep. Krausman and Hervert (1983) reported that sheep were "greatly disturbed" by aerial locations under 50 m and "slightly disturbed" by flights at 50-100 m. Woolf (1968) conducted aerial surveys for bighorn sheep in YNP and found that the sound of the aircraft caused the "major element of fear." He stated that the

noisier, higher powered and faster Cessna 180, 182, and 205 always caused greater alarm in bighorn sheep. I also noticed greater disturbances from Cessna fixed-wing aircraft compared to Piper Super Cubs.

Even when overt reactions are not witnessed, there is information that suggests movements after aerial locations may greatly increase. A study, utilizing conventional VHF collars and GPS units, found that Mountain goats moved 70 % more in the 24 hours following aerial locations compared with undisturbed periods (Poole and Heard 1998).

Currently, the YNP fire crew accounts for the majority of helicopter activity. During the past 10 years tourist flights in other National Parks have increased dramatically, and they may increase in YNP. In Grand Canyon National Park there are estimates of over 40,000 flights per year (Stockwell et al. 1991), and in Glacier National Park there have also been large increases in helicopter sightseeing flights.

Helicopter flights caused considerably greater disturbance than fixed-wing aircraft. Running was rarely a response by bighorn sheep to fixed-wings but was seen during 7 of the 8 observations when helicopters were present. In YNP there are no regulations for helicopter traffic in relation to wildlife disturbances. The regulations that exist are designed around human safety concerns. A minimum 1000-ft flight altitude over populated areas and 500 ft over any other areas is given as a guideline for film crews and tourist flights. Stockwell et al. (1991) recommended minimum flight altitudes in the Grand Canyon of 250-450 m. A more recent study in the Yukon Territory provides a detailed model for calculating minimum setback distances and flight altitudes relative to

elevations frequented by bighorn sheep. For populations of concern, a minimum set back distance of 3.5 km and a relative elevation of 1000 ft are recommended (Frid 1998).

McMinn Bench Group

The McMinn Bench ewe group used the core EWR area more frequently than all the other ewe groups. The close proximity to the town of Gardiner makes bighorns in this area highly visible and accessible to visitors year round. The disturbance frequency of the McMinn Bench group (7.5 %) was substantially greater than that of other groups, since they are exposed to more photographers, hikers, fishermen, road traffic, and greater frequency and proximity to aircraft.

High elevation summer ranges were found on the east cliffs of Sepulcher Mountain. Aircraft and hikers on trails that follow open grassy ridges are probably the only disturbances that may occur on Sepulcher Mountain.

The migration to spring lambing areas by the McMinn Bench ewe group and their subsequent return to Mount Everts caused repeated road crossings near Eagle Nest Rock during June and July. Most overt reactions to humans and road traffic were observed within several months of lambing in the 150-m road buffer. Road crossings occurred most frequently during the afternoon, during peak traffic hours, by ewes that moved from Sepulcher Mountain to McMinn Bench in one day.

Any construction activities on the Gardiner-Mammoth road should occur after July to allow lambs to mature and most ewes to move to higher late summer elevations.

The construction of an elevated bridge or underpass at Eagle Nest rock would greatly reduce the disturbances these ewes currently face and address problems associated with ever increasing vehicle traffic.

Ward et al. (1973) found that Interstate 80 in Wyoming was a barrier to elk movements. In Glacier National Park an underpass (3-8 m high x 23 m wide x 11 m) was constructed for mountain goat crossings (Singer and Doherty 1985). The construction of an underpass should be located on traditional crossing routes (Reed et al. 1975), and not be confining (Ward et al. 1980). Fencing and/or sheer walls need to be incorporated into the design to encourage the use of the underpass and keep sheep off the road. A designated pullout for traffic to keep people at an appropriate distance from the crossing area is highly recommended (Singer and Doherty 1985)

Ram Groups

Ram groups I observed included both yearlong residents of the EWR and migratory units. The only noted disturbances for rams occurred on McMinn Bench (4.6 % overall disturbance rate). During the fall, numerous photographers often spent most of the day following groups of rams (often at close distances). Rams usually seemed undisturbed, but the frequency and number of photographers may cause an accumulation of small disturbances. Summer ranges on Quadrant Mountain currently receive few potential disturbances since they are far from any roads and closed to off trail hiking.

Rattlesnake Butte Ewe Group

This group had the lowest percentage of observed disturbances (2.9 %). During the winter and for much of the summer the group occupied an area 3 - 4 km from the road and main flight corridor and 0.5 km from the nearest hiking trail. Lambing sites were located 5 - 8 km east up the Black Canyon.

Deckard Flats Ewe Group

This ewe group primarily inhabited an area outside the Park boundary and had a mid-level of disturbance of 5.4 %. They sometimes came in contact with domestic dogs (one ewe was blinded in one eye from an attack) as well as hunters and people on horseback. In addition, the group spent several months in close proximity to the highway near La Duke Springs, where one yearling ewe was hit by a car. Lambing locations occurred at Bear Creek in 1997 (close to the Yellowstone River hiking trail) and farther up the Black Canyon in 1998. There is a flight path, up the Black Canyon, taken by aircraft moving east into YNP that could disturb ewes on Deckard Flats and Rattlesnake Butte, both during lambing and during the winter.

Mount Washburn Ewes (Summer Range)

This group is probably exposed to the greatest degree of human activity because they spent the winter on McMinn Bench and the summer on Mount Washburn. The current human activity on Mount Washburn does not seem to be limiting access to any resources, but may be altering natural behavior.

After lambing along cliffs on the west side of the Yellowstone River, the ewes moved up to Mount Washburn by mid to late June. During the summer, the group of ewes and lambs seemed to become more habituated to humans and eventually “begged” from visitors both on the road and hiking trails. Approximately 50 % of all observations occurred with human presence. Group locations occurred primarily in the alpine meadows and burned white-bark pine stands. Snow drifts and seeps provided water sources throughout the summer in numerous locations.

Use of the road corridor occurred along a $\frac{3}{4}$ -km section, primarily during August and September during late afternoon hours. The bighorn sheep rarely cross the road, although they did stay on the road edge for considerable periods of time. The proposed widening of the Dunraven Pass should have little impact on the group. Timing of construction activities should occur after July to allow lambs to mature and the group to become more mobile. Roadside designs could reduce the availability of forage along roads, which may be attracting sheep in late summer. The migrations made by this group occurred before and after the peak traffic season. The heavy use of the road corridor by the sheep near Tower Falls and Calcite Springs in October should be carefully considered if changes in road closures occur. Interestingly, the group seemed to lose interest in begging once they returned to the winter range.

Consequences and Indicators of Disturbance

Disturbance from human activities can increase investments in antipredator behavior and physiological stress. These costs can be evaluated in terms of direct energetic expenditures, lower foraging efficiency and higher heart and metabolic rates (Berger et al. 1983, MacArthur et al. 1982, Stockwell and Berger 1991, Bleich et al. 1994, Cote 1996). Escape behavior or flight is the most obvious cost energetically. Even when escape distances are short (10-50 m) there are other costs involved (Frid 1998). MacArthur et al. (1982) found heart rates in bighorn sheep were elevated 6.3 times longer than the overt response of escaping. At some level, disturbances and increased stress could lead to poor body condition and possibly decreased reproductive potential. Several studies have found signs of decreased reproductive success in vertebrate populations experiencing disturbances (Joslin 1986, Yarmoloy et al 1988, Harrington and Veitch 1992).

If disturbance were a factor over a long period of time, it could reduce recruitment and poor recruitment could lead to smaller group sizes. My study was too short to determine long term effects of disturbance, but all groups on the EWR were small, and poor recruitment occurred in all ewe groups during 1996 and 1997. There were no obvious differences in habitat, predation levels and environmental factors during winter between the groups I monitored. Disturbance levels were quite different. The 3 indices of responses to disturbance I monitored were: 1) behavioral activity (an indicator of energetic expenditures and overt disturbance rates), 2) parasite loads (a possible

indicator of stress, immune system response and reproductive potential), and 3) the hormone corticosterone (an indicator of stress). The relationship between these indices and disturbances varied among groups.

Behavioral Activity

Bighorn sheep were most active in the evening during both summer and winter. The greatest level of activity occurred during the winter (72.5 %). This is extremely close to what Geist (1971: 272) found (72 % active) with Stone's sheep during the winter. Diurnal activity periods reported in the literature vary from 2-4 (Davis 1938, Geist 1971:263, Sayre and Seabloom 1994). Most studies report the highest activity periods in late afternoon and evening, especially during the winter when activity appears to shift away from colder morning hours (Blood 1963, Geist 1971:262). There was a significant difference in the activity levels between summers (1997 = 67 %, 1998 = 59 %). The reason for the variation between summers is unclear. The summer of 1997 was a wetter summer with presumably higher forage quality. In 1998 ewes had more lambs and may have spent less time moving away from secure cover.

The only significant difference in activity levels ($P = 0.0197$) was noted between the McMinn Bench ewe group (7.5 % of observations had disturbances) and Rattlesnake Butte ewe group (2.9 % of observations had disturbances). These groups were more similar in habitat quality, semi-migratory status, predation levels, and proximity to each other than to other groups.

Lungworm Larvae Shedding

There are no data comparing fecal larvae counts with infection intensity in bighorn sheep (Festa-Bianchet 1988). In domestic sheep, gastrointestinal nematode eggs have been correlated with infection intensity (Douch et al. 1984). Forrester and Singer (1964) reported higher larvae levels in herds with more lungworm lesions in the lungs, but the relation between lesions and infection intensity is unknown.

Lungworm larvae shedding in bighorn sheep has long been hypothesized as an indicator of stress, immune system response, and reproductive potential. A sheep under nutritional, reproductive, or physiological stress should shed more larvae than 1 with the same level of infection but not under stress (Fougier-Tower and Onderka 1988, Festa-Bianchet 1991). First-stage larvae are less likely to survive with a strong immune response (Butterworth 1984).

Climatic factors (both seasonal and long term) have been proposed as regulating intensity of lungworm infections (Forrester and Senger 1964, Forrester and Littel 1976, Wishart et al. 1980). Seasonal range use (and thus migratory status) may also be important in the level of infection and reinfection of bighorn sheep (Wishart et al. 1980). Festa-Bianchet (1988) correlated poor maternal behavior, short suckling bouts and reproductive status to LPG levels. In addition, Festa-Bianchet (1988) found LPG levels could not be explained by climatic factors and were not a reliable gauge of herd health, but may be useful in predicting lamb survival.

Using Baermann techniques, I replicated as closely as I could the methods employed in 3 other studies in the region. Differences in data analyses methods make

complete comparisons difficult. Worley et al. (1988) compared prevalence of lungworms in several separate bighorn populations in Montana over a period of 10 years and found levels ranging from 62 % to 96 %. I found the prevalence of infection on the EWR to be 85 %. Keating (1982) conducted the only other test of the EWR group and reported prevalence of 95 % ($n = 95$). Arnett et al. (1993) reported mean LPG levels in rams and ewes in the Cinnabar herd during several winters (rams = 194 ± 34 , ewes = 112 ± 17). I found ewes to have greater levels than rams but found similar means for both sexes (rams 105 ± 20 , ewes 135 ± 18).

When tLPG levels (cube transformed beaker method) were analyzed for differences among groups there were no significant differences found. However, post hoc tests indicated that the McMinn Bench group had significantly lower tLPG levels than the Rattlesnake Butte group. I found significant differences between sexes (ewe > ram), which is dissimilar from other studies (Festa-Bianchet 1988, Arnett et al. 1993). The yearly shedding cycle of both ewes and rams was similar, but ewes had more variability. The greater variation in female tLPG levels during the summer can probably best be explained by increased stress due to pregnancy and lactation (Festa-Bianchet 1989) or to changes in range use, herd structure and exposure (Wishart et al. 1980).

Corticosterone Levels

Reduced resistance to disease has been related to endocrine responses in mammals (Breazille 1988, Kelley 1988). Bighorn sheep are susceptible to pneumonia, which many researchers believe is related to increased frequency and duration of

disturbances (Onderka and Wishart 1984, Spraker et al. 1984, Harlow et al. 1987). Previous studies used measures of plasma cortisol, which may be questionably elevated during the collection process due to anticipation of bleeding or stress related to capture (Turner 1984, Miller et al. 1991). In controlled experiments, bighorn sheep bled near the end of a 10 – 15 minute sampling period (< 2 min per sample) had significantly higher levels of plasma cortisol than the first bighorn sheep sampled (Miler et al. 1991). I used a non-invasive technique of collecting fecal pellets to determine the yearly cycle of corticosterone in free ranging bighorn sheep.

When matched pairs of tLPG and log corticosterone levels were compared there was very little relationship ($n = 333$, $r = 0.0124$, $P = 0.822$), even when sexes were examined separately. This may indicate that lungworm shedding rates are not closely related to stress if corticosterone is a valid indicator of the overall environmental stress experienced by an individual bighorn sheep.

Corticosterone and Social Structure

Population density has also been proposed as a stress factor responsible for regulating populations by acting upon the immune system (Dunbar 1992). Social stress may increase with the level of intraspecific interactions. Geist (1971:72) reported the highest concentrations of sheep in both the fall and spring, with the spring concentrations almost twice the size of the fall. During the winter, social interactions become rare as sheep conserve energy (Gesit 1971:260). One could hypothesize that social interactions increase as density of sheep on a range increase.

This may explain the seasonal cycles I found in corticosterone levels in YNP. The decline of corticosterone levels during the winter in both ewes and rams, may indicate that corticosterone is not a good indicator of depletion of forage quality or quantity or cold temperatures. It has been documented that female corticosterone levels increase during pregnancy in captive sheep (Belden et al. 1990, Miller et al. 1991). However, the large jump in May corticosterone levels in both ewes and rams could be a response to increased social activity. The higher corticosterone levels found in YNP ewes, is different from the higher ram plasma cortisol levels reported by Turner (1984).

In bighorn sheep social structure, the adult rams are dominant and treat all other individuals as females. Dominance is often determined by age (Creel et al. 1992) or body and horn size (Geist 1971:131). Geist hypothesized that dominant rams only acted sexually and that subordinates initiated aggressive acts mostly among themselves. Fighting occurs year round, not for female access but for dominance. Females behave like juveniles, unless in estrus, when they act like a subordinate young male. The young males in turn mimic behavior of females (Geist 1971:153). It is easy to see why corticosterone levels in young males and females are very similar. The lower level of corticosterone found in dominant rams is similar to studies of dominants and subordinates in primates and rodents (Christian and Davis 1964, Blanchard et al. 1995). However, Creel et al. (1997) found that dominants have higher levels of corticosterone in African wild dogs (Lycaon pictus).

Corticosterone and Disturbance

Wildlife managers are often concerned about increased disturbances of animals caused by research activities. The corticosterone levels of collared and uncollared bighorn sheep were virtually identical, indicating that collars did not contribute to added stress in individual bighorn sheep. Creel et al. (1997) also found that collars did not increase corticosterone levels in African wild dogs.

Human related disturbance factors have been examined with corticosterone or cortisol levels for only a few species of vertebrates. Spraker (1984) related human disturbances to a massive bighorn sheep die-off in Colorado. Four sheep collected during this die-off had cortisol serum levels from 7.3 to 13.6 ng/ml. Spraker (1984) assumed normal cortisol levels to be around 5 ng/ml. Harlow et al. (1987) reported resting plasma cortisol levels of 6 ng/ml for tame and 25 ng/ml for wild bighorns. The influence of the collection method on the plasma levels makes comparisons of plasma cortisol difficult. Belden et al. (1991) exposed captive wild and hand-raised bighorn sheep to different types of disturbances. Results indicated that approximately the first month of exposure to a new disturbance was the most detrimental to immune system function and that habituation may occur with factors that are predictable. Miller et al. (1991) reported fecal cortisol levels for hand raised bighorns to be around (7.5 ng / g, baseline) and (12-13 ng / g, ACTH challenged).

Due to the problems related to plasma sampling, fecal samples should prove a more effective way to accurately monitor levels of cortisol or corticosterone. Wasser et al. (1997) found higher fecal corticosterone levels in male spotted owls (Strix

occidentalis caurina) closer to timber management activities and in females when young are fledging. My results indicate similar findings with higher corticosterone levels found for groups of bighorn sheep exposed to more human related disturbances.

Other Conditions Potentially Affecting Population Status

The low recruitment during the 1980's and 1990's and inability of the bighorns on the EWR to recover from the Chlamydia epizootic has many managers concerned. During the 2 years of this study I was able to assess recruitment and mortality. The 8 known mortalities between 1996 and 1998 exceeded the recruitment in the population during the same time period. The lamb:ewe ratios varied dramatically between the 3 years. Lamb:ewe ratios based on adult ewes on the EWR (9:100 1996, 6:100 1997, and 52:100 1998) were much lower than those found by Keating (1982) on the Cinnabar winter range (88:100 1979, 71:100 1980).

High elk numbers (1998 estimate 11,736, Mack pers. commun. NPS) may be involved with the low recruitment of bighorn sheep on the EWR. Interspecific competition with elk is often cited as detrimental to bighorn sheep (Buechner 1960, Woolf 1968, Oldenmeyer et al. 1971, Constan 1972, Barmore 1980, Kasworm et al. 1984, Picton 1984, Keating 1985, Singer 1991). Elk hunting and harassment on agricultural lands directly north of the park may cause elk to pool unnaturally along the YNP boundary in the winter (Houston 1982, Keating 1985).

After the Chlamydia epizootic Keating (1982) proposed 3 scenarios following the bighorn die-off that would explain the level of interspecific competition between elk and bighorn sheep. 1) the bighorn sheep population recovers rapidly to 150-200 individuals after several years indicating minimal interspecific competition with elk, 2) the population grows but stabilizes at a lower median level indicating that moderate sheep-elk interactions may occur, 3) the population stabilizes at around 60 individuals similar to numbers counted prior to the pre-elk reduction program when elk numbers may have had a negative influence on bighorn sheep. Keating's third scenario is very similar to what has occurred in the population. Kasworm et al. (1984) and Singer and Norland (1991) also found that elk and bighorn sheep had the greatest degree of winter diet overlap among ungulates in north central Montana and YNP, which might suggest interspecific competition.

With similar food habits in winter (Kasworm et al. 1984) and orders of magnitude more elk than bighorn sheep, interspecific competition for forage (at least during severe winters) would provide a simple explanation for poor population performance in bighorn sheep (Buechner 1960, Oldenmeyer et al. 1971, Barmore 1980). However, direct forage competition may not be the main problem. Singer and Norland (1995) estimated that during a 3-year period approximately 45 % of the forage escaped herbivory on the northern winter range of YNP. Bighorn sheep may be more suited to utilizing smaller microhabitats inaccessible to elk (Meagher pers. comm.). A sheep faced with starvation can decrease this risk by increasing either the mean amount of food obtained or the protein content in the vegetation consumed. The increased risks taken to obtain food can

increase the probability of predation (McNamara and Houston 1987). Sinclair (1985) examined the relationships of 9 species of herbivores in the Serengeti and determined that predation played as important a role in structuring the community as interspecific competition.

The large numbers of elk and winter carcasses on the EWR may also result in high predator densities that may be more limiting and detrimental than interspecific competition. While population trends of predators in YNP are not well known, there is evidence that many predators such as golden eagles, coyotes and mountain lions have increased in the northern Yellowstone ecosystem during the past 10 years (Legg et al. 1996, Murphy 1998). The introduction of wolves into YNP has reduced coyote densities in some regions and possibly pushed them into areas with greater human presence (such as the EWR).

Further supporting the hypothesis that predation plays a role in limiting the recovery of this population is the decline of bighorn sheep outside YNP where interspecific competition with elk is lower. Legg (1996) and Murphy (1998) found instances of mountain lion predation on bighorn sheep both in and out of the Park. Recent studies have recorded selective predation by mountain lions on bighorn sheep in British Columbia, California, and Alberta (Harrison et al. 1988, Wehausen 1996, Ross et al. 1997). The documentation of mountain lion kills may be biased towards adult sheep since lambs can be rapidly consumed and are therefore difficult to confirm. An intensive study on lion-bighorn interactions revealed that lions were selecting lambs over adult bighorn sheep (Ross et al. 1997). Unfortunately, the study utilized lambs collared in

August, leaving many questions about mortality in the first 2 months after parturition. Scotton (1998 in press) and Haas (1988) marked lambs within several days of birth and attributed the majority of lamb mortality (up to 96 %) to coyote predation within the first few weeks of life.

Haas (1990) reported the occurrence of alloparenting on the National Bison Range (NBR), Montana, and proposed that allonursing may be an evolutionary response to high predation levels. In YNP, allonursing behavior was seen during each summer in 3 of the 4 ewe groups.

The possibility exists that the EWR bighorn population exists in a multi-equilibrium system (Ostovar and Irby, In Press). The population remained over 150 individuals for more than 10 years and now seems stuck in a “predator pit” at around 60 individuals (Seip 1992), typical of a multi-equilibrium system (Dublin et al. 1990) (Fig. 1). An increase in alternate prey (in this case elk) can increase predation by the resultant numerical increase of predators in the system. This has been described with expanding moose (*Alces alces*) populations and subsequent decline of woodland caribou (*Rangifer tarandus*) due to wolf predation (Bergerud and Elliot 1986, Seip 1992). In a similar case, the increase of wood bison (*Bison bison athabasca*) in the Mackenzie Bison Sanctuary may have exacerbated predation on moose (Gates and Larter 1990).

CONCLUSIONS

The bighorn sheep of Yellowstone National Park are a highly visible and important resource. Many questions still remain concerning the status and health of the EWR population. The interspecific competition debate will probably continue for many years. If bighorn sheep are experiencing a “predator pit,” then one would expect the situation to remain unchanged until the system experiences a large perturbation. It is clear that if poor lamb recruitment continues there will be cause for concern. Managers need to keep in mind the potential accumulation of detrimental factors impacting the population of bighorn sheep on the EWR.

The use of noninvasive techniques proved very productive and will hopefully serve as a model for future studies. The accessibility of the EWR groups allowed detailed information to be collected on lungworm larvae and corticosterone fluctuations, which are unavailable for any other wild populations of bighorn sheep. Several important findings were identified.

- 1) Lungworm larvae levels were not correlated to corticosterone levels. This may indicate that lungworm parasite loads play a minor role in the effect they have on the overall environmental stress experienced by bighorn sheep during certain times of the year.
- 2) The effect of winter (temperatures and forage quality and availability) did not raise corticosterone levels.
- 3) The large May increase in corticosterone in both ewes and rams may indicate that social interactions may have significant effects on corticosterone levels.

- 4) The migratory Mount Washburn ewe group had the greatest degree of human contact but one of the lower levels of disturbances. Indicating that bighorn sheep can habituate to certain types of human activity and may be more disturbed by other activities.
- 5) The McMinn Bench ewe group had significantly higher levels of activity, corticosterone and disturbance rates than the Rattlesnake Butte group. Over 50 % of these disturbances were related to aircraft.

My observations indicated that widening the Dunraven Pass road was unlikely to have major impacts on bighorn sheep, but that the Gardiner-Mammoth road realignment needs to be carefully considered. Placement of the road over McMinn Bench could interfere with range use or increase disturbances in 3 distinct groups. The realignment of the road to the west of the Gardner River (including an underpass near Eagle Nest Rock) should be considered as a suitable alternative.

Yellowstone National Park and the Department of Transportation should be commended for their proactive approach in evaluating the potential conflicts between bighorn sheep and road realignments. Additional steps need to be taken by Park managers to establish aircraft flight regulations that consider impacts to wildlife. The development of a study utilizing fecal corticosterone to test the effects of aircraft on bighorn sheep would help quantify levels of disturbance. This would help managers create regulations concerning minimum set back distances and altitudes for different types of aircraft.

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