

INVESTIGATIONS INTO REPRODUCTION BY EWES  
OF A ROCKY MOUNTAIN BIGHORN SHEEP HERD IN WYOMING

E. Tom Thorne, Wyoming Game and Fish Department, University Station, Box 3312, Laramie, WY

Elizabeth S. Williams, Wyoming State Veterinary Laboratory, University of Wyoming, Box 950, Laramie, WY

Walter F. Williams, Department of Animal Science, University of Maryland, College Park, MD

Gary Butler, Wyoming Game and Fish Department, Dubois, WY

ABSTRACT

A 3 year study was conducted on reproduction of Rocky Mountain bighorn sheep in the BLM-Sheep Ridge herd at Whiskey Basin, Dubois, Wyoming. Thirty-four ewes were individually marked at capture. Blood progesterone levels in late winter were used to detect pregnancy. Ewe distribution in June, after the lambing period, was used as an indicator of nursing and early lamb survival. Captive bighorns were used to further evaluate the efficacy of progesterone analysis for pregnancy diagnosis. A blood progesterone level of  $> 2$  ng/ml during the 2nd and 3rd trimesters was used as a positive test, and sensitivity was determined to be 92 percent and specificity 88 percent. Progesterone data indicated 16 percent (4/25) of the wild ewes were not pregnant in February 1981; 16 percent (3/19) were not pregnant in January 1982, 6 percent (1/16) were not pregnant in March 1982; and all (10) were pregnant May 1983. Distribution of ewes in June suggested at least 9 of 24 (38%) study ewes were without lambs in 1981, 5 of 34 (15%) were lambless 1982, and 2 of 30 (7%) were barren in 1983. Of 4 ewes tested for progesterone and/or relocated each year, two probably reproduced every year, one probably did not successfully reproduce any year, and one was apparently unsuccessful for two years and was pregnant the third year. Of 14 ewes tested twice by progesterone analysis and/or relocated in June, 8 (57%), were judged pregnant both years, 3 (21%) probably did not reproduce either year, and 3 (21%) were apparently pregnant one year but not another. Lamb:ewe ratios were generally higher than in previous years. No consistent pattern of alternate-year-reproduction was demonstrated. Possible causes of poor reproduction considered include diseases and parasites, forage production on winter range during the summer as an indication of summer nutrition, forage utilization on winter range, and ram:ewe ratios on winter range.

INTRODUCTION

Low lamb:ewe ratios indicate poor reproductive success in many sheep (*Ovis canadensis* and *O. dalli*) populations of North America (Berwick 1968, Morgan 1970, Horejsi 1972, Shackleton 1973, Stelfox 1974, Thorne et al. 1979). But causes of poor reproduction are difficult to determine.

Heimer (1978) studied a population of Dall sheep undergoing a slow, steady decline and documented alternate-year-reproduction by ewes. In the Dry Creek, Alaska herd, the mean lamb:ewe ratio was .30 among both marked and unmarked ewes from 1972 through 1974. Observations during consecutive summers revealed only 7 percent of the marked ewes were accompanied by a lamb each summer; 53 percent led lambs during alternate summers, and 40 percent were without lambs during two consecutive summers. Only seven of 15 ewes were pregnant when collected during winter. Forage conditions in the Dry Creek area were relatively poor, and Heimer (1978) described an alternate-year reproduction cycle as the cause of the population decline. Lambs were weaned at about 1 year of age, and he felt ewes grazing on inadequate forage did not breed or carry pregnancy to term while raising a lamb because of the effects of depleted energy reserves.

Among BLM-Sheep Ridge sheep of Wyoming studied in 1975 through 1978, large groups of barren ewes were observed very early in summer, and some mature ewes apparently did not go to lambing grounds each spring or stayed a very short time (Thorne et al. 1979). Presence of dry (nonlactating) ewes in those barren groups indicated reproductive failure, very early neonatal mortality, or very late conception and suggested some form of alternate-year-reproduction.

Alternate-year-reproduction is not unique to mountain sheep. It has been seen in red deer (*Cervus elaphus*) on Scottish hill land in a nutritionally inadequate habitat where hinds remain anestrus and fail to breed the year following a successful pregnancy and lactation. Mitchell and colleagues (1976) felt this to be related to body condition and weight as mediated by lactation and forage conditions.

Although Heimer (1978) implied prolonged suckling and lactational infertility as the mechanism causing alternate-year-reproduction among the Dall ewes at Dry Creek he (1982) recently suggested their poor reproductive performance may be due to an improper ratio of mature to immature rams and breeding of yearling ewes that are physically and physiologically unprepared. Hence, the strain of raising a lamb as a 2-year-old results in nutritional and lactational anestrus during the rut of their 2nd year and a cycle of alternate-year-reproduction (Heimer, pers. commun. 1984).

Disproportionately large numbers of young rams may result in harrassment and breeding of young ewes at a higher rate than occurs with a normal young:old ram ratio (Heimer 1982). In 1945, Pulling (1945) who studied desert bighorns (*O. c. nelsoni*), suggested overbreeding of estrous ewes by six or more rams caused over exertion and temporary infertility leading to reproductive failure that year. He stated "practical observers" commonly thought overbreeding due to too many rams harrassing ewes was a cause of poor reproduction. A mechanism mediated by prolactin has been demonstrated in domestic sheep (*Ovis aries*). Stress induces prolactin secretion in ruminants (Forbes et al. 1975, McNeilly 1980) which has antigonadal activity and suppresses behavioral estrus (Kann et al. 1976, Walton et al. 1977, Whitehead and McEwan 1980). Also among domestic sheep, the mere presence of dominant rams has an inhibitory effect upon sexual performance of subordinate rams (Lindsay et al. 1976), and an audience effect undoubtedly influences breeding behavior of bighorn rams. Geist (1971) suggested the inhibitory presence of

large rams prevents excessive harassment of ewes by young, inexperienced rams.

Among domestic sheep, the presence of rams affects onset and synchronization of estrus (Fraser 1968, Redford and Watson 1957, Watson and Redford 1960). Nichols (1978) suggested there may be a similar effect with an earlier and shorter rut occurring in the presence of older mature rams among Dall sheep. Bunnell (1980) noted two or three estrous cycles in Dall sheep. Often there is no estrus in domestic ewes associated with the 1st ovulation of the breeding season. This is apparently due to lack of exposure of the brain to progesterone, which is necessary if estrogens secreted by the ovarian follicle are to cause behavioral estrus (Van Tienhoven 1983). Among Bunnell's (1980) Dall sheep, survival was greatest in lambs conceived during the 2nd cycle. Ewes bred during the 1st cycle were younger than those conceiving later. Ewes giving birth to early lambs risk neonatal mortality due to adverse weather and inadequate milk for the lamb if green-up is delayed.

There are other plausible causes of poor reproduction. Jorgensen and Wishart (1982) demonstrated that among bighorns on Ram Mountain, Alberta a high number of mature ewes during the rut is followed by a lower percent of 2-year-old ewes giving birth to lambs. They felt the number of mature ewes, when high, may influence breeding of yearling ewes by behaviorally suppressing them or, when there are relatively few mature ewes, the attention of rams may be diverted to yearling ewes.

Bunnell (1982) and Thompson and Turner (1982) showed the breeding period of northern mountain sheep is cued to photoperiod and timed to maximize the advantages to lambs of vegetation green-up and summer growing period. Lamb survival is associated with timing of parturition and dependent upon plant phenology (Bunnell 1982). A delayed green-up, with a shorter growing season, adversely affects lamb growth and survival. On Ram Mountain neonatal mortality was influenced by maternal nutrition and by weather at the time of lambing (Jorgensen and Wishart 1982). Maternal nutrition, as evidenced by fecal nitrogen levels, was positively and significantly correlated with green-up. Nutrition late in gestation and during lactation is the major influencing lamb birth weight and rate of growth. These ultimately determine lamb fitness to survive the rigors of winter. Management, of course, cannot control timing of green-up.

Overall nutritional status influences reproductive success in many ways. In domestic ewes, previous nutrition is important in timing onset of estrus and poor nutrition may prolong gestation (Sadleir 1969). Delayed estrus or late parturition would result in bighorn lambs at the end of the growing season which had not reached a desirable body size before winter. Reproductive performance of red deer has been related to forage quality of the hind's home range (Guinness et al. 1978) and to weight of the hind at rut (Hamilton and Blaxter 1980). This is primarily a reflection of quality and quantity of summer forage. Winter feed also has been shown to be important to fetal development and growth and survival of the newborn in many species, including elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), and domestic sheep (Verme 1962, 1965; Thomson and Thomson 1949, Thorne et al. 1976), and undoubtedly is of great importance to bighorns. In Alaska, Nichols (1978) felt a Dall sheep herd he studied responded with increased lambing success to increased winter forage made available by a reduction in population.

During a previous study of the BLM Ridge-Sheep Ridge bighorns, suckling by lambs occasionally was observed in winter and by short yearlings in June (Thorne et al. 1979). Suckling causes a neurogenic stimulus that results in elevated levels of the hormone prolactin which in turn causes lactational ovarian inactivity in women, beef cattle (*Bos taurus*), swine (*Sus scrofa*), and domestic sheep. Only when lactation ceases and prolactin declines is normal ovarian cyclicity reestablished (Wagner and Oxenreider 1971, McNeilly 1980, McNeilly et al. 1982). In other animals, such as dairy cows and dairy goats (*Capra hircus*), normal ovarian activity and ovulation can and do occur in spite of prolonged elevated prolactin levels (McNeilly et al. 1982).

Red deer are a species in which reproductive performance is influenced by lactation. Although plane of nutrition and photoperiod are generally considered mediators of prolactin secretion (Forbes et al. 1975), Loudon et al. (1983) recently showed that frequent and prolonged suckling increases prolactin and results in lactational infertility. In hinds on a low plane of nutrition, there is an increase in suckling frequency by calves in response to low milk production. Frequent and prolonged suckling, in conjunction with increased levels of plasma prolactin, results in prolonged anestrous and delay or failure to breed at the normal time. Prolactin is controlled partially by suckling frequency, i.e. a direct relationship between suckling frequency and prolactin secretion. This response is independent of physical condition of the hinds. However, delayed or late conception has been demonstrated to occur in red deer in poor body condition and/or lactating as compared to hinds in good physical condition and dry (Mitchell and Lincoln 1973). It is possible these mechanisms caused poor reproductive performance among bighorn ewes of the BLM-Sheep Ridge herd in the past years. Observations of ewes still being suckled long after their lambs should have been weaned lends strong supporting evidence.

The BLM-Sheep Ridge Rocky Mountain bighorn herd contains 300 to 400 sheep and winters along Jakey's Fork Canyon on the Whiskey Basin Game Winter Range in Fremont County, Wyoming. This herd and its habitat, along with the Torrey Rim bighorn population which is similar in size and with which it shares the Whiskey Basin Winter Range, have been described (Butler 1977, Thorne et al. 1979). Although the BLM-Sheep Ridge herd has grown since efforts to protect and enhance its winter range began in the mid 1950's, lamb:ewe ratios have generally been low. In 1979 the population appeared in stable condition and of moderately low quality (Thorne et al. 1979). A limited number of trophy rams are shot annually and some lambs, ewes, and young rams are trapped for transplant. In recent years, an effort has been made to hold sheep numbers below carrying capacity with a resultant 65 percent utilization of winter range forage by sheep. Efficient trapping techniques were developed in the late 1970's, and size of the winter range utilized was increased by baiting sheep into previously unused areas beginning in the winter of 1981-82.

Upon leaving winter range, pregnant Rocky Mountain bighorn ewes typically move to secluded lambing areas where lambs are born. After a short time, nursery bands consisting of lambs and lactating ewes are formed, and they remain in areas characterized by readily available forage and precipitous escape cover until lambs are strong enough for migration to summer range. Simultaneously, yearlings, 2-year-olds, ewes without lambs (dry), and young rams form barren groups which later join with lactating ewes and lambs for

summer migration. Thus, for 3 to 4 weeks in early summer, female bighorn bands are split into two distinct groups (Geist 1971). This pattern was evident among BLM-Sheep Ridge ewes, and lambing grounds and nursery areas used by lactating ewes and more open, less precipitous spring-fall ranges, used by dry ewes were identified (Thorne et al. 1979).

Progesterone is a steroid hormone primarily secreted by the corpus luteum of the estrous cycle and pregnancy. Blood progesterone levels have been used to diagnose pregnancy in cattle, goats, domestic sheep, elk, white-tailed deer, and bighorn sheep (Bassett et al. 1969, Ramsay and Sadleir 1979, Vogelsang et al. 1977, Whitehead and McEwen 1980, Holdsworth 1981, Weber et al. 1982). In one study using three Rocky Mountain bighorn ewes, plasma progesterone levels associated with cyclic luteal function were 3.2 to 4.0 ng/ml and during pregnancy reached levels of 13.3 to 23.2 ng/ml until just before parturition (Whitehead and McEwen 1980). In an earlier study with bighorns, Ramsay and Sadleir (1979) suggested a progesterone threshold level of 2 to 3 ng/ml during the last 2/3 of gestation was diagnostic of pregnancy.

The purpose of this 3 year study was to use blood progesterone levels as an indication of pregnancy and ewe association with nursery or barren groups as an indication of nursing and early lamb survival to determine if alternate-year-reproduction was occurring among ewes of the BLM-Sheep Ridge bighorn sheep population. Captive bighorns were used to further evaluate the efficacy of progesterone analysis for pregnancy diagnosis. A secondary objective was to explore possible causes of poor reproduction among BLM-Sheep Ridge bighorn ewes.

#### METHODS

An apple pulp-baited drop-net trap (Erickson 1970, Schmidt 1976, Schmidt et al. 1978, Emmerich 1982) or chemical immobilization with projectile syringe-delivered etorphine<sup>1</sup> and acepromazine<sup>2</sup> (Thorne 1971, Thorne 1982a) were used to capture bighorn ewes in February 1981, January and March 1982, and May 1983. With the exception of 22 ewes trapped for transplant in January 1982, all captured ewes were individually marked with a small domestic sheep-sized, numbered, plastic ear tag; a small numbered, metal ear tag; and a numbered neck band. During the 2nd and 3rd years, an attempt was made to recapture ewes that previously had been captured for this study.

Heparinized and clotted venous blood samples obtained from captured ewes were kept cool until centrifuged for plasma and serum collection 6 to 24 hours after collection. Samples were frozen (-20C) until analyzed for progesterone using a modified radioimmunoassay protocol (Knight et al. 1977) with progesterone antibody (courtesy Dr. J. L. Fleeger, Texas A&M University) characterized by Wise et al. (1975). The radioimmunoassay was validated by demonstrating parallelism to standards by internal standards and by sample dilution. Assay data were computed using a modification of a program

<sup>1</sup> M-99 Etorphine<sup>R</sup>, Lemon Company, Box 30, Sellersville, PA 18960

<sup>2</sup> Acepromazine<sup>R</sup>, Ayerst Laboratories, 685 Third Avenue, New York, NY 10017

developed by English (1981). Inter and intraassay coefficients of variation were 14.1 percent and 13.0 percent, respectively. Using modifications of the criteria of Ramsay and Sadleir (1979), progesterone values of  $> 2$  ng/ml of serum or plasma were considered to indicate pregnancy in the last 2/3 of gestation.

One 3/4 bighorn x 1/4 mouflon (*O. musimon*) hybrid and six bighorn sheep at the Wyoming Game and Fish Department Sybille Wildlife Research Unit were similarly tested for pregnancy. Periodic blood samples were obtained while the animals were manually restrained. During estrus, some ewes had access to bighorn rams, and the control of captivity allowed pregnancy to be confirmed by birth of a lamb. Twenty-three recently captured bighorn ewes held at the Wild Animal Disease Center, Colorado State University, Ft. Collins were also tested for serum progesterone levels in 1979 and 1980.

Sensitivity and specificity of blood progesterone values as a diagnostic test for pregnancy were determined (Rogan and Gladen 1978, Brown and Newman 1979). Sensitivity was defined as the chance a test will be positive ( $> 2.0$  ng/ml) when the animal is pregnant and specificity was defined as the chance a test will be negative when an animal is not pregnant.

During 8 to 12 June 1981, 17 to 20 June 1982, and 26 June to 1 July 1983, observations were made with the aid of 7x35 binoculars and 20-power spotting scopes in areas known to be used during those times by sheep of the BLM-Sheep Ridge population (Thorne et al. 1979). Attempts were made to locate and identify neck-banded ewes previously captured and pregnancy tested in order to determine if they had lambs.

Comparisons between mean progesterone values in serum and plasma and between mean progesterone values of pregnant and nonpregnant sheep in different stages of gestation were made using Student's t test. Relationships between summer forage production on winter range as an indication of summer nutrition, winter forage utilization, and rams:100 ewes on the lamb:ewe ratio the following winter were examined by determining the Pearson product moment correlation coefficient and by simple linear regression. Lamb:ewe and ram:ewe ratios and winter range forage production and utilization data were obtained from Wyoming Game and Fish Department files, Whiskey Basin Big Game Winter Range and Lander, Wyoming.

Some captured BLM-Sheep Ridge bighorns were also tested for important diseases and parasites. Sera were tested for Leptospira interrogans serovars hardjo, pomona, icterohemorrhagiae, canicola, and grippityphosa (Leptospirosis) antibodies using a microscopic agglutination test. Sera were also tested by immunodiffusion for antibodies against ovine progressive pneumonia virus. In addition, ewes were tested for Campylobacter fetus jejuni (campylobacteriosis or vibriosis) using an indirect hemagglutination serologic test and culture techniques by vaginal washings using nutrient broth inoculated into Clark's Campylobacter transport medium. Ear swabs were taken in 1982 and 1983 and examined for of Psoroptes sp. scabies mites.

## RESULTS

### PREGNANCY DIAGNOSIS

Gestation in bighorn sheep is about 176 days (Geist 1971, Blunt et al. 1977, Whitehead and McEwan 1980). Peripheral progesterone levels greater than 2 to 3 ng/ml during the last 2/3 of pregnancy were suggested by Ramsay and Sadleir (1979) as diagnostic of pregnancy in bighorns. Using 7 June as an arbitrary, but probable, date when over 50 percent of lambs were born (Honest and Frost 1942, Thorne et al. 1979, Bunnell 1982), the breeding peak was 14 December with 9 February the end of the first trimester of pregnancy (58 days) of BLM-Sheep Ridge ewes.

Depending upon tests anticipated to be conducted upon a blood sample, logistics, and personal preferences, blood may be collected into anticoagulant, e.g., heparin, or into a "dry" tube and allowed to clot. Plasma or serum are then collected by centrifugation. Progesterone analyses may be conducted on either form, and we had the opportunity to analyze plasma and serum from the same blood samples of 45 bighorns. There was no significant difference in circulating progesterone when plasma or serum was used for the analysis ( $P > .05$ ). Similarly, Ramsay and Sadleir (1979) showed little difference in progesterone levels when determinations were made on plasma and serum. There were three blood samples in which plasma progesterone was  $> 2$  ng/ml and serum progesterone was below that level; two serum progesterone level were  $> 2$  ng/ml and the paired plasma progesterone was  $< 2$  ng/ml. On these few occasions, the highest value was used to diagnose pregnancy.

Breeding date and day of gestation the date blood samples were collected from captive ewes were determined by calculating back from the known date of a lamb's birth. At Sybille (Table 1), nine blood samples were obtained during the last 2/3 of pregnancy; eight were correctly diagnosed using a blood level of 2.0 ng/ml progesterone as a threshold. The exception was "Sis" on 5 May 1983 with a circulating progesterone level of 0.7 ng/ml on the 139th day of gestation. Three of eight blood samples obtained during the first trimester of pregnancy had peripheral progesterone levels below 2.0 ng/ml (Table 1). As the Wild Animal Disease Center (Table 2), 17 blood samples were obtained from ewes later shown to have been in the latter 2/3 of gestation; only one was not diagnosed correctly. Blood was obtained 40 times from captive ewes shown later not to be pregnant (Figure 1); serum or plasma levels exceeded 2.0 ng/ml nine times. These blood samples were obtained during December through February when some ewes still may have been cycling. There was a definite rise in mean circulating progesterone levels in nonpregnant ewes which approached or exceeded 2 ng/ml during January and February (Figure 1).

Plasma or serum progesterone values for pregnant and nonpregnant ewes in the first trimester were not significantly different ( $P > .05$ ); however, progesterone values for pregnant ewes in the second trimester were significantly higher ( $P < .0001$ ) than for nonpregnant ewes during the same time period (Figure 2). Data from nonpregnant ewes were not available for the last trimester of pregnancy.

Table 1. Serum and/or plasma progesterone levels of captive, mature, female sheep at the Sybille Wildlife Research Unit, Wyoming.

Sheep	23 Jan '81	9 Mar '81	22 Dec '81	27 Jan '82	26 Feb '82	2 Apr '82	8 Dec '82	Feb '83	10 Mar '83	5 May '83
	Serum and plasma ( ) progesterone in ng/ml and day of gestation if pregnant									
Sara	3.4	1.5	0.4	1.9(2.9)	3.7(3.5)	0.3(1.2)	(2.8)	2.3 49 da	5.9 86 da	9.8 142 da
Sis	1.2	1.7	4.0	2.8(2.0)	1.2(0.8)	0.4(0.9)	(0.5)	3.1 46 da	7.7 83 da	0.7 139 da
Heather <sup>1</sup>	1.9 23 da	2.8 66 da	0.2	1.3(1.1)	4.6(0.8)	0.2(0.7)	-	-	-	-
Wildone	2.1 42 da	2.1 85 da	-	-	-	-	-	-	-	-
W-50	-	-	0.8 11 da	2.5(2.7) 42 da	2.9(3.2) 77 da	3.3(4.8) 112 da	1.4 2 da	2.0 57 da	5.9 94 da	-
Kelly	-	-	1.5	0.7 (0.9)	0.3(0.1)	(0.7)	-	-	-	-
W-48	-	-	1.9	1.7(2.0)	1.2(0.9)	0.6(0.1)	-	-	-	-

<sup>1</sup> Heather was a 3/4 bighorn x 1/4 mouflon hybrid; all others were bighorn.



Table 2. Serum progesterone levels of captive, female bighorn sheep at the Wild Animal Disease Center, Colorado

Sheep	Age	Serum progesterone in ng/ml and day of gestation [ ] if pregnant								
		1979 29 Mar	23 Aug	26 Sept	7-26 Oct	14 Feb	29 Mar	10-12 Apr	12 Aug	7-8 Sept
CTBT9	4	8.2(112)			0.6(0)					
C3BT75	4	3.6(115)			0.7(0)					
CTBT6	3	0.9(0)				0.4(0)				
CTR38	5	4.2(89)	0.5(0)							
CTR48	5	8.4(2126)		0.4(0)	0.9(0)					
CTBT77	Mat	4.4(109)								
CTBT32	4	1.7(111)								
CTBT35	3	6.1 (116)								
CTBT46	4	4.0(P) <sup>1</sup>								
CTO8	4				0.1(0)					
CTBT33	3				0.1(0)					
CRBT51	7						6.4(P)			
CRGT19	3						3.4(P)			0.3(0)
CRGT17	Mat						5.9(P)			
CRGT21	3						2.7(112)			0.4(0)
CRR20	2						0.7(0)			
CRR23	8						7.2(136)			
CRR15	3						0.1(0)			
CRR26	4						4.1(126)			
CRCT22	3						5.8(131)			
CRR17	7							13.4(P)		
CRR44	3							7.8(P)		
CRR22	6								0.7(0)	

<sup>1</sup> (P) = Confirmed to be pregnant at necropsy, date of gestation undetermined; (0) = not pregnant.

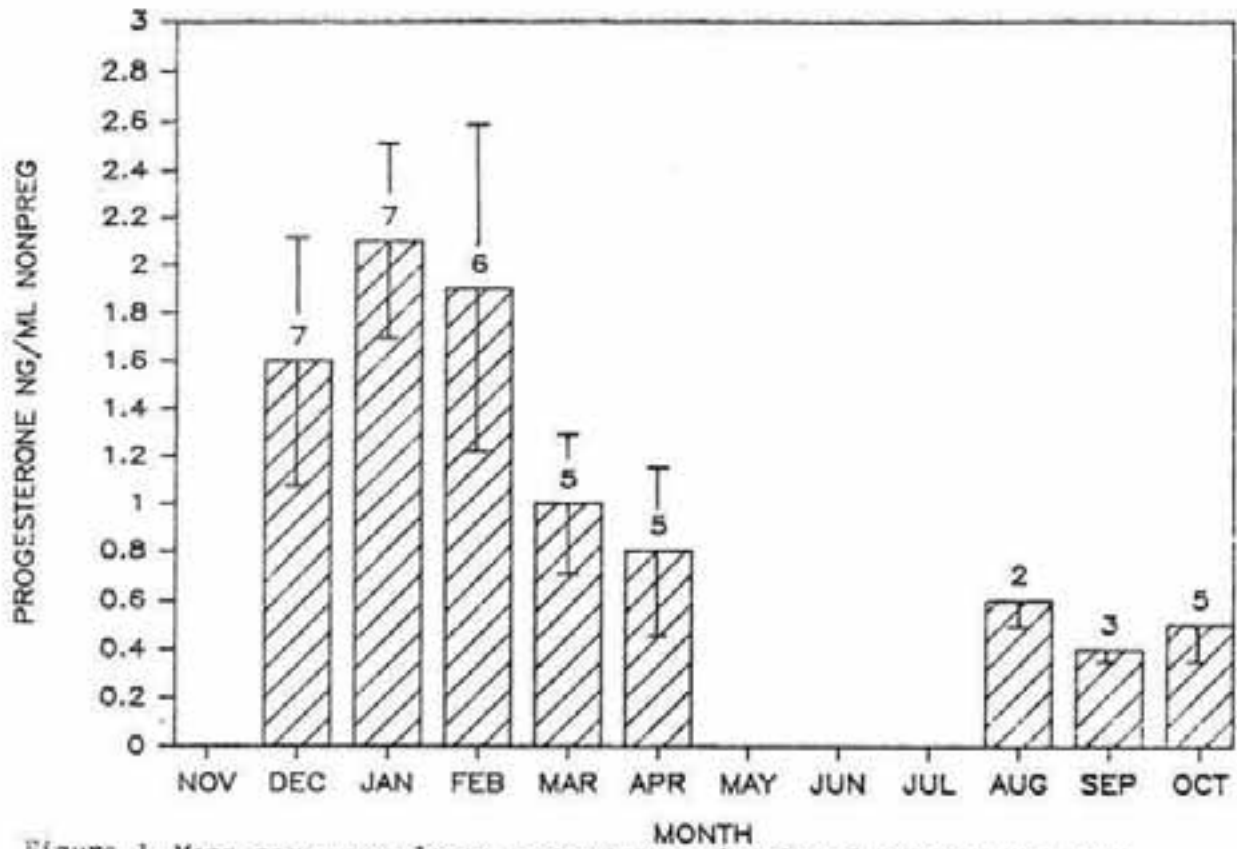


Figure 1. Mean serum or plasma progesterone levels of nonpregnant ewes throughout the year.

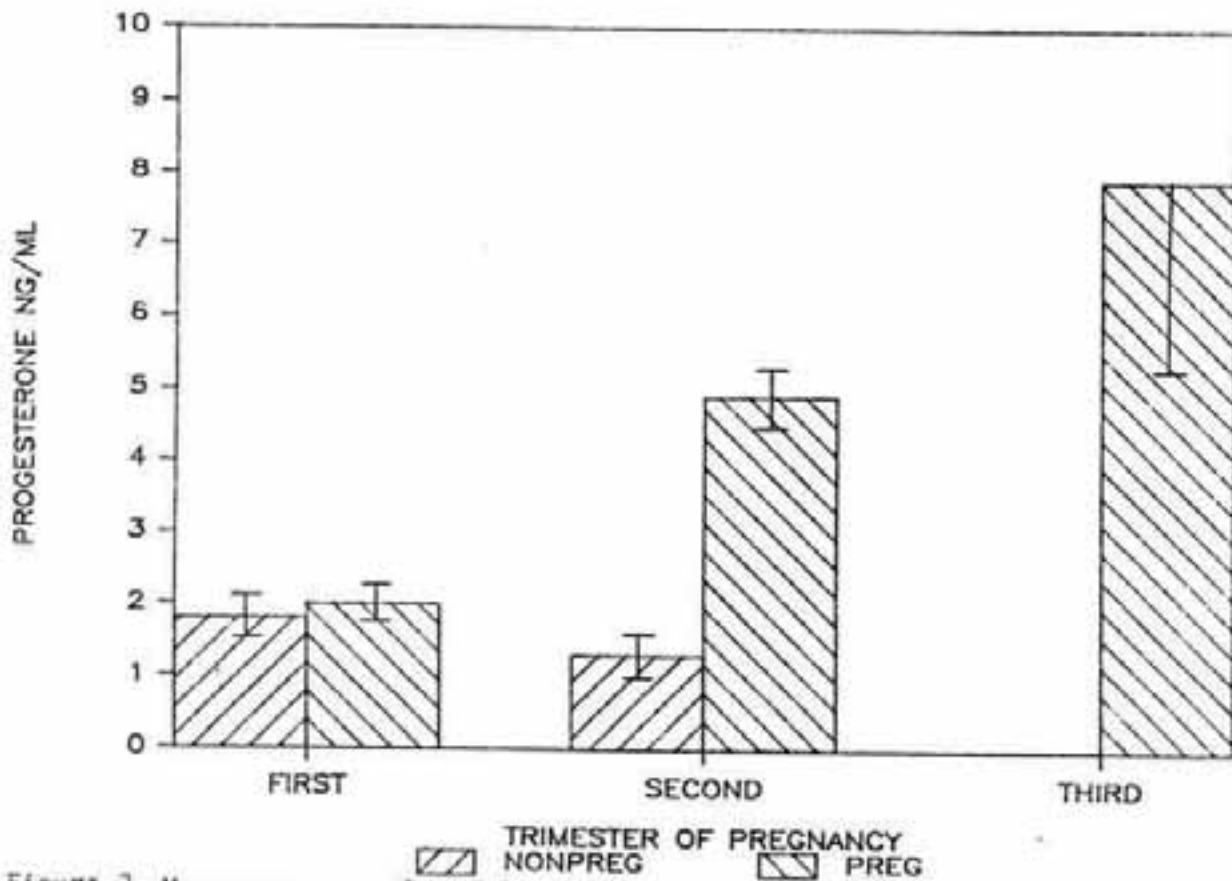


Figure 2. Mean serum or plasma levels for pregnant and nonpregnant ewes during each trimester of pregnancy.

Sensitivity of serum or plasma progesterone assay using  $> 2$  ng/ml during the last two thirds of pregnancy as diagnostic of pregnancy was 92 percent; specificity using the same criterion was 88 percent. Thus we would expect about 12 percent false positive results and 8 percent false negative results using this test for pregnancy in bighorns.

Progesterone levels were determined on 73 occasions from free-ranging ewes from the BLM-Sheep Ridge herd in 1981 (25), 1982 (38), and 1983 (10). In 1981, blood was collected between 3 and 21 February (Table 3) which is late in the 1st or early in the 2nd trimester of gestation, the period when Whitehead and McEwan (1980) demonstrated a temporary decline in progesterone levels. Four (16%) of 25 ewes were diagnosed as not pregnant. In two sheep, progesterone levels were 2.1 ng/ml; they may have been cycling instead of pregnant, and one of these ewes (Y-16) was seriously injured in the drop-net and euthanized. Necropsy revealed she was not pregnant.

In January 1982, 22 ewes captured for transplant were tested during the 1st trimester; 19 (86%) had progesterone  $> 2.0$  ng/ml and were diagnosed pregnant; three (14%) were diagnosed as not pregnant. However, these sheep were tested shortly after the usual breeding season and some may have been cycling. Sixteen additional sheep were tested during the 2nd trimester in March; only one (6%) was not pregnant (Table 3). Overall pregnancy rate in 1982 was 89 percent (34/38).

Ten ewes were tested in May of 1983 and all were judged to be pregnant (Table 3). One of these ewes died in May and was pregnant when necropsied.

Nine ewes were tested in 2 consecutive years. One was judged not pregnant either year, seven were pregnant both times, and one was pregnant in 1982 but not in 1981. Five ewes were tested in 1981 and again in 1983. Four were pregnant both years; one was pregnant in 1983 but not in 1981. One ewe was tested three times and was pregnant each year.

Attempts were made to locate and observe neck-banded ewes in June of 1981, but inclement weather made observations in precipitous lambing grounds difficult. Eight or 9 neck-banded ewes were observed 1 to 3 times each. None definitely had a lamb (Table 3), as judged from previous work which noted marked distribution differences between lactating ewes and dry ewes without lambs on spring-fall ranges (Thorne et al. 1979). Three of five ewes determined by progesterone levels as not pregnant in February 1981 were observed in June (Table 3). Only six of the 19 judged pregnant in February were reobserved in June. These ratios (3/5 and 6/19) are significantly different at the 95 percent confidence level (McDonald et al. 1981). This suggests those ewes identified with barren groups were without lambs.

In June 1982, six neck-banded ewes were observed. Five were without lambs based on their presence in barren groups; one ewe was tested by progesterone analysis in March and judged pregnant, another was diagnosed not pregnant. Of four neck-banded ewes observed in June 1983, two had lambs and both were diagnosed pregnant by progesterone analysis in May. Two were without lambs; one tested pregnant in May, the other was not captured.

Table 3. Pregnancy test results on captured sheep and judgement made in June if observed sheep had a lamb

No.	Age When Captured	1981		1982		1983	
		Progesterone Date ng/ml	Test <sup>1</sup>	Progesterone Date ng/ml	Test <sup>1</sup>	Progesterone Date ng/ml	Test <sup>1</sup>
Y-1	4+	3 Feb 7.1	+	5 Mar 7.5(7.5) <sup>3</sup>	+	N.O.	N.O.
Y-2	Old	3 Feb 3.7	+	N.O.		N.O.	N.O.
Y-3	3	3 Feb 7.4	+	4 Mar 3.7(10.2)	+	N.O.	N.O.
Y-4	4	3 Feb 6.4	+	N.O.		N.O.	N.O.
Y-5	4+	3 Feb 9.4	+	N.O.		N.O.	N.O.
Y-6	4+	3 Feb 4.9	+	N.O.		N.O.	N.O.
Y-7	3	3 Feb 13.0	+	N.O.		N.O.	N.O.
Y-8	3	3 Feb 1.0	-	N.O.		N.O.	N.O.
Y-9	4+	10 Feb 16.0	+	N.O.		N.O.	N.O.
Y-10	+	10 Feb 1.5	-	N.O.		N.O.	N.O.
Y-11	11	10 Feb 5.5	+	N.O.		L.T	N.O.
Y-12	3	10 Feb 4.5	+	N.O.		L.T	N.O.
Y-13	4+	10 Feb 3.6	+	16 Mar (9.0)	+	N.O.	N.O.
Y-14	10+	10 Feb 2.1	-	N.O.		N.O.	Sent to Utah 6 Jan, 1983
Y-15	3	10 Feb 9.3	+	N.O.		N.O.	Dead
Y-16	Old	10 Feb 2.1	+	Dead-February not pregnant		N.O.	Dead-pregnant in January
Y-16a	4+	10 Feb 1.2	-	4 Mar 0.5(0.1)	-	N.O.	N.O.
Y-17	4+	10 Feb 13.0	+	N.O.		N.O.	N.O.
Y-18	3	10 Feb 9.6	+	N.O.		N.O.	N.O.

Table 3. Continued

No.	Age When Captured	1981		1982		1983	
		Progesterone ng/ml	June observation <sup>2</sup>	Progesterone ng/ml	June observation <sup>2</sup>	Progesterone ng/ml	June observation <sup>2</sup>
Y-19	4+	10 Feb 10.0	+	13 Mar 7.1(5.7) <sup>3</sup>	+	N.D. <sup>4</sup>	N.O.
Y-20	4+	10 Feb 2.7	+	N.D.		N.D.	N.O.
Y-90	4+	10 Feb 1.6	-	13 Mar 5.1(9.9)	+	N.D.	N.O.
Y-22	9	21 Feb 5.5	+	N.D.		9 May 3.6	Dead-May Pregnant
Y-23	4	21 Feb 5.5	+	N.D.		N.D.	N.O.
Y-24	3	21 Feb 10.0	+	N.D.		N.D.	N.O.
G-39	5	N.D.		13 Mar 6.4(10.2)	+	N.O.	L
W-28	5	N.D.		13 Mar 4.6(5.8)	+	N.O.	N.O.
Y-88	3	N.D.		14 Mar 8.6(7.9)	+	N.O.	N.O.
Y-89	3	N.D.		14 Mar 11.6(8.7)	+	N.O.	N.O.
Y-92	1	N.D.		14 Mar 3.3(6.4)	+	N.O.	N.O.
Y-91	5	N.D.		15 Mar 7.5(9.8)	+	N.O.	N.O.
Y-93	6	N.D.		15 Mar 4.3(4.0)	+	N.O.	N.O.
Y-95	5	N.D.		15 Mar (4.7)	+	N.O.	N.O.
R-45	5	N.D.		15 Mar (4.7)	+	N.O.	N.O.
R-44	3	N.D.		16 Mar 7.4(6.2)	+	N.O.	N.O.

<sup>1</sup> Judged pregnant if serum or plasma progesterone > 2.0 ng/ml.

<sup>2</sup> Not observed, N.O.; without a lamb, W.O.; with a lamb, L.; unable to determine, ?.

<sup>3</sup> Serum progesterone (plasma progesterone)

<sup>4</sup> No data, N.D.

Table 3 summarizes proesterone data and summer observations. Data on reproduction were obtained for 14 ewes during 2 years and for four ewes during all 3 years. Of 14 ewes with data for 2 years, eight (57%) were determined pregnant or as having a lamb both years, three (21%) were determined pregnant or as having a lamb on 1 of those 2 years, and three (21%) sheep were barren both years. Of the four sheep tested and/or observed all 3 years, two were determined pregnant all 3 years, one ewe was without a lamb 2 years and pregnant 1 year, and one ewe probably did not successfully reproduce any year.

Of 41 ewes whose samples were assayed for progesterone after 9 February, 34% (14) were observed in spring. Of those tested and reobserved that spring, there was 43 percent agreement between the pregnancy determination by progesterone analysis and evidence of the ewe having a lamb or being barren in June. Where there was disagreement, the ewe was diagnosed pregnant by progesterone analysis and was dry when observed in summer suggesting neonatal mortality.

Winter range forage production in the summer, winter range forage utilization, and rams/100 ewes were not significantly correlated ( $P > .05$ ) with lambs/100 ewes the following winter (Table 4). There was a marked increase ( $P = .0531$ ) in lamb/ewe ratios during the period 1981-84 as compared to the period 1975-1979 (Table 4).

#### DISEASES AND PARASITES

Sera of 21 ewes were tested by the microscopic agglutination test against five serovars of Leptospira interrogans. Although there were some low reactions, none was higher than 1:160 and none was regarded as significant.

One ewe (Y-16) accidentally killed during trapping and subsequently necropsied had histopathologic changes suggestive of ovine progressive pneumonia. However, none of the ewes trapped in 1981, including Y-16, had detectable antibodies to ovine progressive pneumonia. Histopathologic changes of ovine progressive pneumonia and those induced by chronic Protostrongylus spp. lungworm infection may be similar.

Cultures for Campylobacter spp. were prepared from seven ewes in 1981, 21 in 1982, and 15 in 1983. A Campylobacter sp. grew from the vaginal washing of one ewe (Y-5) in 1981; however, before the organism could be identified, it was overgrown and killed by contaminating organisms. Sera of 28 ewes were tested for antibodies against goat and sheep isolates of C. fetus jejuni; five reacted at 1:160 and all others produced lower reactions. Serum from the ewe from which Campylobacter sp. was recovered was not available for serology.

Ten ewes captured in 1982 and 20 in 1983 were negative for Psoroptes sp. scabies mites when both ears were checked by swab.

Table 4. Forage production, forage utilization, ram:ewe ratios and lamb:ewe ratios from 1974 - 1984 at BLM-Sheep Ridge, Whiskey Basin, Wyoming.

Winter	Mean forage prod. previous season (kg/ha)	Mean forage util. during winter (%)	Rams/100 ewe		Lambs/100 ewe		
			All <sup>1</sup>	Immature <sup>2</sup>	Yearlings included	Yearlings excluded	
1974-75	365	78	22	ND <sup>4</sup>	ND	19	ND
1975-76	467	63	ND	ND	ND	8	ND
1976-77	467	55	5	ND	ND	24	ND
1977-78	264	63	ND	ND	ND	ND	ND
1978-79	319	64	26	ND	ND	49	ND
1979-80	342	54	ND	ND	ND	ND	ND
1980-81	459	69	ND	ND	ND	50	ND
1981-82	460	75	43	38	13	60	71
1982-83	291	89	68	59	10	32	39
1983-84	680	ND	49	45	7	41	44

<sup>1</sup>Yearling ewes included

<sup>2</sup>Yearling through class II

<sup>3</sup>Class III and IV

<sup>4</sup>No data, N.D.

## DISCUSSION

### PREGNANCY DIAGNOSIS

Peripheral blood progesterone in domestic ewes remains uniformly low except during the luteal phase of the estrous cycle and during pregnancy (Bassett et al. 1969, Thorburn et al. 1969, Moore et al. 1972, Walton et al. 1977). Bighorn sheep, with the exception of a temporary decline in progesterone between 50 and 80 days of gestation, exhibit a similar pattern (Ramsay and Sadleir 1979, Whitehead and McEwan 1980). Thorburn et al. (1969) reported plasma progesterone levels during the 1st 4 days of the nonpregnant cycle in the domestic ewe were below 0.4 ng/ml, increased to 1.5 to 2.5 ng/ml during days 4 through 9, and then declined rapidly on days 14 to 15 to about 0.1 ng/ml at estrous. In domestic sheep during the nonpregnant cycle, progesterone levels peak at 2.5 to 5.6 ng/ml (Thorburn et al. 1969, Sarda et al. 1973, Yuthasastrakosol et al. 1975); and progesterone did not exceed 4 ng/ml in three bighorn ewes studied by Whitehead and McEwan (1980) and our ewes tested during the breeding season. Bunnell (1980) described two or three distinct estrous cycles in Dall sheep during the breeding season, and Rocky Mountain bighorns presumably also cycle two or three times, which would take about 48 days. For routine pregnancy diagnosis, differentiation between low progesterone levels in nonpregnant ewes and high levels in pregnant ewes is more important than precise, specific determinations of circulating hormone levels (Sugden 1978, Ramsay and Sadleir 1979) or examining fluctuations associated with the estrous cycle.

Circulating progesterone remains elevated in pregnant domestic and bighorn ewes. In domestic ewes, plasma progesterone levels during the 1st 50 days of pregnancy are 2 to 3 ng/ml and are not significantly higher than during the luteal phase of the estrous cycle. After 50 days of pregnancy, plasma progesterone increases 2 to 5 times (Bassett et al. 1969). In bighorn ewes, an elevated level may be reached by 50 days of gestation (Whitehead and McEwan 1980). Progesterone concentrations between days 60 and 80 in bighorn ewes studied by Whitehead and McEwan (1980), and in our ewes, did not fall below 2.5 ng/ml. Thus, during the 1st 2 months after the breeding season progesterone levels below 2.0 ng/ml in bighorn sheep indicate no pregnancy or very early gestation. Three of our captive ewes had 0.8 to 1.9 ng/ml progesterone between 2 and 23 days of gestation (Table 1). During the 1st trimester, 2 to 6 ng/ml should indicate pregnancy or the luteal phase of the estrous cycle. Progesterone in excess of 6 ng/ml should reflect pregnancy. False diagnoses of pregnancy may occur at levels < 6 ng/ml during the 1st 3rd of gestation. Pregnancy diagnosis early in gestation, while some ewes may still be exhibiting estrous cycle, was unreliable and impractical. As demonstrated by Ramsay and Sadleir (1979), Whitehead and McEwan (1980), and this study, a threshold of 2.0 ng/ml progesterone during the latter 2/3 of gestation is quite diagnostic.

### REPRODUCTION BY BLM-SHEEP RIDGE BIGHORNS

In contrast to many of the years to this study, reproduction among BLM-Sheep Ridge bighorns in 1981, 1982, and 1983 was generally high and there was no consistent pattern of alternate-year-reproduction. Although a few



study ewes did not reproduce every year, most marked and unmarked ewes were pregnant. BLM-Sheep Ridge bighorns seemed to be responding to management activities; and current, relatively low reproductive losses apparently occur as prenatal, postnatal, or summer mortalities. We were unable to determine a cause, but population imbalances may be responsible for a few nonpregnant ewes and lamb mortalities.

Except for winter range manipulation and population control, little can be done to improve the nutrition of the BLM-Sheep Ridge bighorns. Although ranges used in spring and fall may be limited, summer ranges seem very adequate (Thorne et al. 1979) and these sheep capitalize upon the advantages of extensive altitudinal migrations (Hebert 1973). Our data failed to show a relationship between forage production on winter range, which we used as an indication of length of growing season, precipitation and forage quality on summer ranges, and, presumably, summer nutrition, and reproductive success.

The most significant management activities influencing BLM-Sheep Ridge bighorns and their nutrition are population control through trapping and transplanting and winter range improvement and expansion. The former has probably reduced the size of the population slightly from the late 1970's and kept the herd within the calculated limits of winter range carrying capacity since the mid 1970's. Since 1975, trapping has removed 566 sheep from the BLM-Sheep Ridge and Torry Rim populations; the majority have been from the former. The intent has been to remove sheep in relation to long term (5 year) forage utilization and hold utilization under 65 percent. This practice, after an expected lag time, likely is responsible more than any other factor for improved productivity since 1979. In addition, range expansion by baiting bighorns to a previously unused area has increased critical winter range and forage by about 20 percent (32.3 ha) since 1981. This has increased the winter range nutrient potential for the herd and likely also has contributed to relatively high lamb production in recent years.

Among BLM-Sheep Ridge bighorns, trapping and transplanting generally removes a cross section of the ewe population along with a few lambs and young rams, and it is very unlikely the number of yearling ewes has ever been high in proportion to mature ewes. Indeed, there is little evidence of ewes lambing on their 2nd birthday among these sheep. If population imbalances acting through behavior to cause reduced reproductive performance among the BLM-Sheep Ridge bighorns, it would almost have to be due to a disproportionately high ratio of young to mature rams. The sex ratio of bighorns normally is about 1:1 and the death rate of rams is low and steady between ages 2 and 8, after which mortality of rams is probably higher than that of ewes. Table 4 shows a low ram:ewe ratio and a high immature to mature ram ratio among sheep from the BLM-Sheep Ridge where rams reach 3/4 curl horn size at 4 or 5 years (Thorne et al. 1979, Table 20). Classification presented in Table 4 are somewhat biased because they were generally conducted toward the end or after rut when some older rams had left the company of ewes; however, it is apparent the young ram segment is disproportionately high in relation to mature rams. Observations during rut when as many as 4 to 6 young rams can be observed harassing ewes in the absence of large rams tends to confirm this. If this is influencing reproductive success, it would be through early birth of lambs or harassment induced temporary infertility, which would not be corrected by reduction of the overall population size or

habitat improvement. Shifting ram age structure toward older, larger rams might improve reproductive performance.

#### DISEASES AND PARASITES

No evidence of scabies or leptospirosis was detected among BLM-Sheep Ridge bighorns. Leptospirosis does cause abortion in some species, including domestic sheep, and mortality in juveniles; but it has not been reported in North American wild sheep (Thorne 1982b). Although not examined in this study, previous studies have failed to reveal the presence of brucellosis, an important reproductive disease of cattle and elk, among bighorn sheep of BLM-Sheep Ridge (Thorne et al. 1979).

Ovine progressive pneumonia is insidious in onset and characterized first by weight loss and, after a course of 3 to 12 months, by death (Cutlip et al. 1978). It is probably transmitted directly from sheep to sheep (Gates et al. 1978, De Boer et al. 1979). Experimentally, ovine progressive pneumonia has been shown to cause resorption or abortion of fetuses early in pregnancy (Cutlip et al. 1982). Many sheep may be persistently infected with virus and have antibodies against it without ever showing clinical signs (Cutlip et al. 1978).

Ovine progressive pneumonia has never been diagnosed in mountain sheep. The small evidence we found was too equivocal to conclude the disease was present in BLM-Sheep Ridge bighorns; however, it should not be ignored. The historic association of mountain sheep with domestic sheep and the contagious nature of ovine progressive pneumonia suggest this disease of domestic sheep could be transmitted to wild sheep. It might not run as long a course in mountain sheep as in domestic sheep because debilitated wild sheep would be unlikely to survive as long as affected domestic sheep. Occasional emaciated, debilitated ewes are observed among BLM-Sheep Ridge bighorns with an appearance similar to domestic ewes with ovine progressive pneumonia; however, these animals are generally felt to be showing the effects of old age. Domestic range ewes with chronic diseases, including ovine progressive pneumonia, which result in debilitation and weight loss also have impaired reproductive efficiency, primarily through lowered fertility and fewer lambs born alive. Lowered fertility is presumed to be due to prolonged disease-induced stress and associated catabolism (Gates et al. 1977).

In domestic sheep, campylobacteriosis is an acute disease characterized by abortion during the last trimester of pregnancy or death of the lamb at or shortly after birth. Although infertility is not a problem, abortion rates among domestic sheep may range from 5 to 70 percent with 25 percent abortion being common (Marsh 1965, Jubb and Kennedy 1970, Dennis 1975, Smibert 1978). Campylobacter fetus is a fragile organism which is killed by exposure to oxygen and difficult to culture on artificial media. The preferred sources for isolation from domestic sheep are bile and cotyledons of the ewe and abomasal content, liver, spleen, and brain of a fetus or lamb. Culture of vaginal washings to diagnose ovine campylobacteriosis is a poor diagnostic technique which was chosen in lieu of aborted lambs and for lack of the preferred tissues for culture. Recovery of Campylobacter sp. from one ewe is not diagnostic because many animals are host to commensal nonpathogenic

Campylobacter spp. It is unfortunate the isolate recovered in 1982 could not be identified to subspecies. Negative cultures from 42 other ewes does not prove campylobacteriosis is not present because the organism is so difficult to cultivate. Five of 28 ewes tested serologically for campylobacteriosis produced low positive reactions; however, these could not be considered diagnostic because higher titers would be expected from actively infected sheep. Campylobacteriosis could be responsible for poor reproduction among mountain sheep, especially in large herds where there would be ample opportunity for transmission.

#### RECOMMENDATIONS

Although the BLM-Sheep Ridge bighorn population has experienced poor reproduction in the past, productivity during this study was improving and by 1983 was relatively good. We feel this was most likely due to management activities since the mid 1970's and, therefore, make the following recommendations.

1. Population control by transplanting in relation to available winter forage should be continued to maintain a healthy herd.
2. Range extension and range improvement should be continued and increased where possible.

Although this study did not confirm presence of diseases adversely affecting health or reproduction of these bighorns, equivocal evidence of two diseases was revealed and the threat of new diseases and widespread transplanting of these bighorns indicate there is no reason for complacency.

3. Surveys for presence of disease and parasites should be continued using the most reliable diagnostic techniques available.

#### ACKNOWLEDGEMENTS

We acknowledge J.M. Emmerich and personnel of District 6, Game Division, Wyoming Game and Fish Department, U.S. Forest Service, and Bureau of Land Management for their assistance with sheep capture and restraint; we also appreciate the help and companionship of friends who accompanied us on spring trips searching for newborn lambs and neck banded ewes. Captive bighorns were cared for and restrained by H.A. Dawson, C.V. Engstrom, and B. Meyer of the Sybille Wildlife Research Unit, Wheatland, Wyoming and personnel of the Wild Animal Disease Center, Ft. Collins, Colorado. The manuscript was reviewed by W.D. Wishart and W.G. Hepworth and we appreciate their comments. Financial support was provided by the Rocky Mountain Conservative Fund and Wyoming Game and Fish Department (Federal Aid in Wildlife Restoration Projects FW-3-R and W-54-D).

LITERATURE CITED

- Basett, J.M., T.J. Oxborrow, I.D. Smith, and G.D. Thornburn. 1969. The concentration of progesterone in the peripheral plasma of the pregnant ewe. *J. Endocrinol.* 45:449-457.
- Berwick, S.H. 1968. Observations on the decline of the Rock Creek, Montana population of bighorn sheep. M.S. Thesis. Univ. of Montana, Missoula. 245 pp.
- Blunt, F.M., H.A. Dawson, and E.T. Thorne. 1977. Birth weights and gestation in a captive Rocky Mountain bighorn sheep. *J. Mammal.* 58:106.
- Brown, J. and M.A. Newman. 1979. Lesions of swine lymph nodes as a diagnostic test to determine mycobacterial infection. *Appl. Environ. Microbiol.* 37:740-743.
- Bunnell, F.L. 1980. Factors controlling lambing period of Dall's sheep. *Can. J. Zool.* 58:1027-1031.
- Bunnell, F.L. 1982. The lambing period of mountain sheep: Synthesis, hypotheses, and tests. *Can. J. Zool.* 60:1-14.
- Butler, G. 1977. Big game winter range, Whiskey Basin Unit, inventory and analysis. Wyoming Game and Fish Dept., Cheyenne. 85 pp.
- Cutlip, R.C., T.A. Jackson, and H.D. Lehmkuhl. 1978. Diagnostic features of ovine progressive pneumonia. *J. Am. Vet. Med. Assoc.* 173:1578-1579.
- Cutlip, R.C., H.D. Lehmkuhl, S.C. Whipp, and A.W. McClurkin. 1982. Effects on ovine fetuses of exposure to ovine progressive pneumonia virus. *Am. J. Vet. Res.* 43:82-85.
- De Boer, G.F., C. Terpstra, D.J. Houwers, and J. Hendriks. 1979. Studies in epidemiology of maedi/visna in sheep. *Res. Vet. Sci.* 26:202-208.
- Dennis, S.M. 1975. Perinatal lamb mortality in western Australia: 5. Vibrionic infection. *Aust. Vert. J.* 61:11-12.
- Emmerich, J.M., M. Hockley, and E.S. Kimber 1982. Electronic release system for drop nets. Proc. Northern Wild Sheep and Goat Council, Ft. Collins, Colo. pp. 83-91.
- English, J.E. 1981. A powerful, yet easy to use, computerized analysis of competitive protein binding and radioimmunoassay data. *Computer Programs in Biomedicine.* 13:225-238.
- Erickson, J.A. 1970. Use of drop net and collars in study of Dall sheep. Proc. Northern Wild Sheep Council, Williams Lake, British Columbia. pp. 20-21.

- Forbes, J.M., P.M. Driver, A.A. El Shahat, T.G. Bozz, and C.G. Scanes. 1975. The effect of daylength and level of feeding on serum prolactin in growing lambs. *J. Endocrinol.* 64:549-554.
- Fraser, A.F. 1968. Reproductive behavior in ungulates. Academic Press, London. 202 pp.
- Gates, N.L., L.D. Everson, and C.V. Hulet. 1977. Effects of thin ewe syndrome on reproductive efficiency. *J. Am. Vet. Med. Assoc.* 171:1266-1267.
- Gates, N.L., L.D. Winward, J.R. Gorham, and D.T. Shen. 1978. Serologic survey of prevalence of ovine progressive pneumonia in Idaho. *J. Am. Vet. Med. Assoc.* 173:1575-1577.
- Geist, V. 1971. Mountain sheep: A study in behavior and evolution. University of Chicago Press, Chicago. 383 pp.
- Guinness, F.E., S.D. Albon, and T.H. Clutton-Brock. 1978. Factors affecting reproduction in red deer (*Cervus elaphus*) hinds on Rhum. *J. Reprod. Fert.* 54:325-334.
- Hamilton, W.J. and K.L. Blaxter. 1980. Reproduction in farmed red deer. 1. Hind and stag fertility. *J. Agric. Sci.* 95:261-273.
- Hebert, D.M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis. Univ. of British Columbia, Vancouver. 357 pp.
- Heimer, W. 1978. Alternate year reproduction in a low quality, declining Dall sheep population: Management considerations. Proc. Northern Wild Sheep and Goat Council, Penticton, British Columbia. pp. 30-40.
- Heimer, W.E., and S.M. Watson. 1982. Differing reproductive patterns in Dall Sheep: Population strategy or management artifact. Proc. Northern Wild Sheep and Goat Council. Fort Collins, Colo. pp. 330-338.
- Honess, R.F. and N.M. Frost. 1942. A Wyoming bighorn sheep study. Wyoming Game and Fish Dept. Bull. 1 126 pp.
- Horejsi, B. 1972. Behavioral differences in bighorn lambs (*Ovis canadensis canadensis* Shaw) during years of high and low survival. Proc. Northern Wild Sheep Council, Hinton, Alberta. pp. 51-73.
- Jorgenson, J.T. and W.D. Wishart. 1982. Ram Mountain bighorn sheep study progress report. Alberta Fish and Wildlife Div., Edmonton. 41 pp.
- Jubb, K.V.F. and P.C. Kennedy. 1970. Pathology of domestic animals. Vol. 1. 2nd ed. Academic Press, New York. 593 pp.

- Knight, J.W., F.W. Bazer, W.W. Tatcher, D.E. Franke, and H.D. Wallace. 1977. Conceptus development in intact and unilaterally hysterectomized ovariectomized gilts: Interrelations among hormonal status, placental development, fetal fluids and fetal growth. *J. Anim. Sci.* 44:620-637.
- Loudon, A.S.I., A.S. McNeilly, and J.A. Milne. 1983. Nutrition and lactational control of fertility in red deer. *Nature.* 302:145-147.
- Lindsay, D.R., D.G. Dunsmore, J.D. Williams, and G.J. Syme. 1976. Audience effects on the mating behavior of rams. *Anim. Behaviour.* 24:818-821.
- Marsh, H. 1965. *Newsom's sheep diseases.* 3rd ed. The Williams and Wilkins Co., Baltimore, Md. 456 pp.
- McDonald, L.L., H.R. Bauer, B.M. Davis, and B. Laby. 1981. Critical regions of an unconditional non-randomized test of homogeneity in 2 x 2 contingency tables. *Applied Stat.* 30:182-189.
- McNeilly, A.S. 1980. The female. *J. Reprod. Fert.* 58:537-549.
- McNeilly, A.S., A. Glasier, J. Jonassen, and P.W. Howie. 1982. Evidence for direct inhibition of ovarian function by prolactin. *J. Reprod. Fert.* 65:556-569.
- Mitchell, B. and G.A. Lincoln. 1973. Conception dates in relation to age and condition in two populations of red deer in Scotland. *J. Zool., Lond.* 171:141-152.
- Mitchell, B., D. McCowna, and I.A. Nicholson. 1976. Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. *J. Zool., Lond.* 180:107-127.
- Moore, N.W., S. Barrett, and J.B. Brown. 1972. Progesterone concentrations in maternal and foetal blood plasma of ewes. *J. Endocrinol.* 53:187-194.
- Morgan, J.K. 1970. Ecology of the Morgan Creek and East Fork of the Salmon River bighorn sheep herds and management of bighorn sheep in Idaho. *Fed. Aid in Wildl. Rest. Res. Compl. Rep. Project No. W-142-R-1, Job Nos. 1, 2, 3, Idaho Fish and Game Dept., Boise.* 155 pp.
- Nichols, L. 1978. Dall sheep reproduction. *J. Wildl. Manage.* 42:570-580.
- Pulling, V.S. 1945. Non-breeding in bighorn sheep. *J. Wildl. Manage.* 9:155-156.
- Ramsay, M.A. and R.M.F.S. Sadleir. 1979. Detection of pregnancy in living bighorn sheep by progestin determination. *J. Wildl. Manage.* 43:970-973.

- Redford, H.M. and R.H. Watson. 1957. The influence of rams on ovarian activity and oestrus in merino ewes in spring and early summer. *Aust. J. Agric. Res.* 8:860-870.
- Rogan, W.J. and B. Gladen. 1978. Estimating prevalence from the results of a screening test. *Am. J. Epidemiol.* 107:71-76.
- Sadleir, R.M.F.S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen & Co., Ltd. London. 321 pp.
- Sarda, I.R., H.A. Robertson, and T.C. Smeaton. 1973. Sequential changes in plasma progesterone levels in the ewe during the estrous cycle, and during pregnancy in intact and ovariectomized sheep. *J. Anim. Sci.* 53:25-34.
- Schmidt, R. 1976. Baiting bighorn sheep with apple pulp and trapping with a drop net. *Proc. Northern Wild Sheep Council, Jackson, WY* pp. 26-34.
- Schmidt, R., W.H. Rutherford, and F.M. Bodenham. 1978. Colorado bighorn sheep-trapping techniques. *Wildl. Soc. Bull.* 6:159-163.
- Shackleton, D. 1973. Population quality and bighorn sheep. Ph.D. Thesis. Univ. of Calgary, Alberta. 227 pp.
- Smibert, R.M. 1978. The genus Campylobacter. *Ann. Rev. Microbiol.* 32:673-709.
- Stelfox, J.G. 1974. Range ecology of bighorn sheep in relation to self regulation theories. *Proc. Northern Wild Sheep Council, Great Falls, Mont.* pp. 67-76.
- Sugden, E.A. 1978. Rapid radioimmunoassay of progesterone in unextracted bovine plasma. *Can. J. Comp. Med.* 42:229-234.
- Thompson, R.W. and J.C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. *Can. J. Zool.* 60:1781-1793.
- Thomson, A.M. and W. Thomson. 1949. Lambing in relation to the diet of the pregnant ewe. *Brit. J. Nutr.* 2:290-305.
- Thorburn, G.D., J.M. Bassett, and I.D. Smith. 1969. Progesterone concentration in the peripheral plasma of sheep during the oestrous cycle. *J. Endocrinol.* 45:459-469.
- Thorne, T. 1971. The use of M99 etorphine and acetylpromazine in immobilization and capture of free ranging Rocky Mountain bighorn sheep. *Trans. N. Am. Wild Sheep Conf., Ft. Collins, Colo.* 1:127-134.
- Thorne, E.T. 1982a Agents used in North American ruminant immobilization. pp. 304-334 in L. Nielsen, J.C. Haig, and M.E. Fowler. eds., *Chemical immobilization of North American Wildlife*, Proc. North American Symposium: Chemical Immobilization of Wildlife. Wisconsin Humane Soc. Inc., Milwaukee.

- Thorne, E.T. 1982b. Leptospirosis. pp. 46-52. In E.T. Thorne, N. Kingston, W.R. Jolley, and R.C. Bergstrom, eds. *Diseases of Wildlife in Wyoming*, Second Edition. Wyoming Game and Fish Dept., Cheyenne.
- Thorne, T., G. Bulter, T. Varcalli, K. Becker, And S. Hayden-Wing. 1979. The status, mortality and response to mangement of the big horn sheep of Whiskey Mountain. Wildl. Technical Rept. No. 7, Wyoming Game and Fish Dept., Cheyenne. 213 pp.
- Thorne, E.T., R.E. Dean, and W.G. Wepworth. 1976. Nutrition during gestation in relation to successful reproduction in elk. *J. Wildl. Manage.* 40:330-335.
- Van Tienhoven, A. 1983. *Reproductive physiology of vertebrates*. Cornell Univ. Press. Ithaca, NY. 491 pp.
- Verme, L.J. 1962. Mortality of white-tailed deer fawns in relation to nutrition. *Proc. Nat'l. White-tailed Deer Symp.*, Athens, GA. 1:15-18.
- Verme, L.J. 1965. Reproduction studies on penned white-tailed deer. *J. Wildl. Manage.* 29:74-79.
- Vogelsang, R.W., R.L. Kirkpatrick, and P.F. Scanlon. 1977. Progesterin levels as indicators of multiple pregnancy in white-tailed deer. *Virginia J. of Sci.* 22:68 (Abst.).
- Wagner, W.C. and S.L. Oxenreider. 1971. Endocrine physiology following parturition. *J. Anim. Sci.* 32 (Suppl. 1): 1.
- Walton, J.S., J.R. McNeilly, A.S. McNeilly, and F.J. Cunningham. 1977. Changes in concentrations of follicle-stimulating hormone, lutenizing hormone, prolactin and progesterone in the plasma of ewes during the transition from anoestrus to breeding activity. *J. Endocrinol.* 75:127-136.
- Watson, R.H. and H.M. Redford. 1960. The influence of rams on the onset of oestrus in merino ewes in the spring. *Aust. Agric. Res.* 2:65-71.
- Weber, B.J., M.L. Wolfe, and G.C. White. 1982. Use of serum progesterone levels to detect pregnancy in elk. *J. Wildl. Manage.* 46:835-838.
- Whitehead, P.E. and E.H. McEwan. 1980. Progesterone levels in peripheral plasma of Rocky Mountain bighorn ewes (*Ovis canadensis*) during the estrous cycle and pregnancy. *Can. J. Zool.* 58:1105-1108.
- Wise, T.H., A.M. Sorensen Jr., and J.L. Fleeger. 1975. Quantitation of deoxycorticosterone and its relationship to progesterone in the pre-partum bovine. *Steroids.* 26:17-18.
- Yuthasastrakosol, P., W.M. Palmer, and B.E. Howland. 1975. Lutenizing hormone, oestrogen, and progesterone levels in peripheral serum of anoestrus and cyclic ewes as determined by radioimmunoassay. *J. Reprod. Fertil.* 43:57-65.