LUMPY JAW IN WILD SHEEP AND ITS EVOLUTIONARY IMPLICATIONS

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LUMPY JAW IN WILD SHEEP AND ITS EVOLUTIONARY IMPLICATIONS

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ABSTRACT: The distribution and prevalence of mandibular osteomyelitis, lumpy jaw, and other dental anomalies in wild sheep were investigated and their biological and evolutionary implications were assessed. Our survey was based on 3,363 mandibles of wild sheep and 1,028 from domesticated varieties. Lumpy jaw is widespread in wild sheep of North America, but it is rare or absent in wild sheep from Eurasia. Among the subspecies of *Ovis* spp. in North American, the thinhorn sheep (*Ovis dalli*) were the most seriously impacted, with a prevalence in Dall's sheep (*O. dalli dalli*) of 23.3% and 29.3% in Stone's sheep (*O. dalli stonei*). Among the bighorns (*O. canadensis*), the Rocky Mountain subspecies (*O. canadensis canadensis*) had a higher rate (12.1%) than other subspecies. Lumpy jaw was not documented in the desert sheep of Baja California (*O. canadensis cremnobates, O. canadensis weemsii*). Based on data from affected thinhorn sheep, it appears there is an inverse relationship between age of a subspecies in a long term evolutionary context and susceptibility to lumpy jaw. In Eurasian wild sheep lumpy jaw is rare or absent with prevalences ranging from 0 to 7.1% among suspecies, and in domesticated breeds the prevalence averaged 5.0%. The impact of lumpy jaw on different age classes or longevity is equivocal, although females are more susceptible than males. Lumpy jaw appears to effect horn development in males.

Key words: Actinomycosis, evolution, horn growth, lumpy jaw, mandibular osteomyelitis, *Ovis* spp., wild sheep.

INTRODUCTION

Dental and mandibular diseases are common in the wild sheep of North America. Blair (1907) first described this problem when six of 12 Stone's sheep (*Ovis dalli stonei*) collected in the Stikine River drainage of northern British Columbia (Canada) were affected. The disease was referred as actinomycosis. Murie (1944), in his extensive studies in Mt. McKinley now Denali National Park (Alaska, USA), examined 829 mandibles of Dall's sheep (*O. dalli dalli*), of which 25.7% were affected. Murie (1944) assumed, as Blair (1907) had, that *Actinomyces bovis* was the causative agent and referred to the disease as "lumpy jaw" because of the similarity of this disease in elk (*Cervus elaphus*), pronghorn antelope (*Antilocapra americana*), domestic cattle, and domestic sheep.

The term "lumpy jaw" in wild sheep has been used as a catch-all for various dental and mandibular anomalies, which may or may not include mandibular osteomyelitis. As a result, lumpy jaw has been reported from many areas of western North America, covering essentially all subspecies of wild sheep except for the desert sheep (*O. canadensis cremnobates*, *O. canadensis weemsii*) of Baja California (Mexico) for which little information exists.

The etiologic agents of classical lumpy jaw are the bacteria that infect and become established in the bones of the oral cavity. *Actinomyces bovis,* which is primarily responsible for lumpy jaw in domestic cattle and sheep, has seldom been recovered from active lesions of wild sheep. Instead, *Arcanobacterium pyogenes*, *Fusobacterium necrophorum*, *Staphylococcus aureus,* and *Streptococcus* spp., have been isolated and characterized (Glaze et al., 1982). Gross lesions of mandibular osteomyelitis include distortion and proliferation of the jaw bones, damage to teeth, abundant scar tissue, and in some cases fistulas draining through the skin (Bunch et al., 1999).

The most extensive survey of lumpy jaw was made in the Yukon Territory (Canada) where 831 mandibles of hunter-killed rams

TABLE 1. Prevalence of lumpy jaw in sheep as documented from museums and other collections worldwide.

Species/subspecies	Number examined	Prevalence
Ovis canadensis canadensis	961	12.1%
Ovis canadensis californiana	301	3.0%
Ovis canadensis nelsoni	100	6.0%
Ovis canadensis mexicana	204	4.4%
Ovis canadensis cremnobates/weemsii	79	0%
Ovis dalli dalli	507	23.3%
Ovis dalli stonei	198	29.3%
Ovis nivicola	68	0%
Ovis ammon ammon	76	0%
Ovis ammon darwini	23	0%
Ovis ammon polii	88	0%
Ovis ammon karelini	36	0%
Ovis ammon hodgsoni	40	0%
Ovis ammon (*unclassified*)	18	0%
Ovis orientalis vignei	32	0%
Ovis orientalis gmelini	6	0%
Ovis orientalis cycloceros	50	7.1%
Ovis orientalis musimon	316	5.7%
Ovis orientalis (*unclassified*)	256	0.4%
Ovis aries	1028	5.0%

were inspected between 1979 and 1985 (Barichello et al., 1989). The sampling was territory-wide in scope, covering all but a few protected sheep populations. The overall prevalence was 37% and varied regionally between 23.5% and 50.0% (Barichello et al., 1989).

This report is a follow-up of the previous Yukon study (Barichello et al., 1989). The objectives of the current investigation were: (1) Define "lumpy jaw"; (2) determine the prevalence and geographic distribution of lumpy jaw in *Ovis* spp. and assess their evolutionary relevance; and (3) interpret the impact of lumpy jaw on both individual animals and populations.

MATERIALS AND METHODS

We inspected mandibles and skulls of *Ovis* spp. specimens in museums, universities, wildlife agencies, and national parks in North America and Europe, to determine the prevalence of lumpy jaw. A total of 4,387 jaws were examined, 3,359 from wild *Ovis* spp. and 1,028 from *Ovis aries.* Single mandibles were used in our assessments, since many of the collection specimens as well as jaws submitted by hunters were not paired. In this survey, we classified lumpy jaw positive specimens as those with osteomyelitis of the mandibles. Dental anomalies alone were not included in our data set. All assessments were done by the senior author. We did not attempt to differentiate the lesions by putative etiologic agents. Our sample was supplemented by information from a long term study of Dall's sheep on Sheep Mountain in Kluane National Park (Yukon Territory) which provided data on 82 mandibles of both sexes and 33 sets of undamaged horns of rams for assessment of age- and sex-specific prevalence of lumpy jaw as well as its possible influence on horn development. Age determination was based upon horn ring counts (Geist, 1966) and horn growth was assessed using the method of Taylor (1962). We used Valdez (1982) and Bunch et al. (1999) classification of wild sheep of the world in our allocation of mandibles to different taxa. *T*-tests were applied to compare horn segment lengths and circumferences of affected and unaffected rams as well as differences in longevity. A value of a set at $P \leq 0.05$ was considered significant (Sokal and Rohlf, 1969).

RESULTS

Lumpy jaw affects most subspecies of North American wild sheep, but is rare or absent in the wild sheep of Eurasia (Table 1). Stone's sheep had the highest prevalence of lumpy jaw (29.3%), closely followed by Dall's sheep with 23.3%. Bighorns are less affected, with considerable variation among subspecies. The Rocky Mountain bighorn (*O. canadensis canadensis*) had the highest prevalence with 12.1%, with the more northern populations approaching the rate of Dall's sheep. The highest rates in bighorn sheep have been reported in the Rocky Mountain national parks in Canada (Table 2). Lumpy jaw is less frequent in more southern Rocky Mountain bighorn populations, but isolated cases have been reported in Washington State (USA) (Dalquest and Hoffmeister, 1948) and Montana (USA) (Couey, 1950). Information provided by biologists about herds in the western USA reveal that lumpy jaw is not a serious problem (G. Erickson, R. Johnson, T. Thorne, and D. Toweill, pers. comm.). The subspecies, *O. canadensis californiana, O. canadensis nelsoni,* and *O. canadensis mexicana* have a lower prevalence of lumpy jaw, and we found no evidence of lumpy jaw in 79 mandibles inspected from desert sheep of Baja California (*O. canadensis cremnobates* and *O. canadensis weemsii*). The reported prevalences of lumpy jaw in North American wild sheep (Table 2) are often higher than in our sample from museum and other collections (Table 1). However, specimens in museum collections are probably more representative for a given subspecies because they are collected from many different populations and areas. On the other hand, reported prevalences for the most refer specifically to affected herds. In Eurasian wild sheep lumpy jaw is rare or absent except for the European mouflon (*O. orientalis musimon*) with a prevalence of 5.7% and the Afghan urial (*O. orientalis cycloceros*) with 7.1%.

Prevalence of lumpy jaw was high in the Sheep Mountain herd of Kluane National Park, (Yukon Territory) (Table 3) with 49% for rams and 76% for females. However, even at this high rate the disease did not appear to result in a lowered life expectancy. There was no statistical difference (P = .65) in the average age at death of

TABLE 2. Reported prevalence of lumpy jaw in North American wild sheep.

Subspecies	Location	Sample size	Prevalence	Author(s)
Ovis dalli dalli	Denali National Park, Alaska	829	25.7%	Murie, 1944
Ovis dalli dalli	Crescent Mountain, Kenai, Alaska	46	40%	Neiland, 1972
Ovis dalli dalli	Dry Creek, Alaska	183	26%	Heimer et al., 1982
Ovis dalli dalli	Sheep Creek, Alaska	107	12%	Heimer et al., 1982
Ovis dalli dalli	Ruby Range, Yukon	9	66.6%	Glaze et al., 1982
Ovis dalli dalli	Yukon (Territory-wide)	831	37%	Barichello et al., 1989
Ovis dalli dalli	MacKenzie Mountains, N.W.T.	95	28%	Kutny and Stenhouse, 1991
Ovis dalli stonei	Stikine River drainage, B.C.	6	50%	Blair, 1907
Ovis dalli stonei	Laurier Pass area, B.C.	9	100%	Sheldon, 1932
Ovis dalli stonei	Nelvis Creek drainage, B.C.	7	71.4%	Luckhurst, 1973
Ovis canadensis canadensis	Banff and Jasper National Park, Alberta	56	66%	Cowan, 1943
Ovis canadensis canadensis	Sheep River drainage, Alberta	21	14.3%	Wishart, 1958
Ovis canadensis canadensis	National Parks, Alberta	79	12.7%	Stelfox, 1976
Ovis canadensis nelsoni	Nevada, Arizona, California	178	18.5%	Alfred and Bradley, 1965
Ovis canadensis nelsoni/mexicana	Arizona (state-wide)	150	20.0%	Glaze et al., 1981

TABLE 3. Age-specific prevalence of lumpy jaw in the Dall's sheep of Kluane National Park, Yukon Territory, Canada.

Age (years)	Affected males	Affected females
2–3	2/3 (67%)	
3–4	0/1 (0%)	1/1 (100%)
4–5	1/2 (50%)	
5–6		1/2 (50%)
6–7	3/4 (75%)	2/2 (100%)
7–8	3/6 (50%)	4/6 (67%)
8–9	4/8 (50%)	1/2 (50%)
9–10	2/8 (25%)	5/6 (83%)
10–11	5/10 (50%)	1/1 (100%)
11–12	2/4 (50%)	2/3 (67%)
12–13	2/2 (100%)	3/4 (75%)
13–14	0/1 (0%)	3/4 (75%)
>14		2/2 (100%)
Total	24/49 (49%)	25/33 (76%)

rams that were affected ($\bar{x}$ = 8.54 yr, n = 24) compared to those not affected ($\bar{x}$ = 8.88 yr, n = 23), nor in affected females ($\bar{x}$ = 10.32 yr, n = 25) compared to others ($\bar{x}$ = 9.75 yr, n = 8) (P = .64). In this population lumpy jaw affected both old and young sheep (Table 3). Two of three rams that died in their 2nd to 3rd year were infected and a 3- to 4-yr-old female had lumpy jaw.

The Kluane study did provide evidence that females are more susceptible to lumpy jaw than males. In Table 5 we have summarized information about sex-specific prevalences. In this study we also pointed to a negative influence of lumpy jaw on horn growth in rams (Table 4). We examined 33 undamaged skulls, 14 from affected rams and 19 from unaffected rams. With the exception of the first year's growth, we observed that rams without lumpy jaw generally had better horn growth in length than affected ones. The differences were not always statistically significant (Table 4). At 10 yr of age the nonaffected ram had horns with an average length of 95.1 cm. The affected ram group averaged 89.9 cm. This relationship was also observed in horn circumference. Rams without lumpy jaw had horns with greater circumferences than affected ones. The greatest difference was observed in

TABLE 4. Horn growth in length and circumference of lumpy jaw affected and unaffected rams in Kluane National Park (Yukon Territory, Canada).

Year class		1	2	3	4	5	6	7	8	9	10	11
Affected rams (n = 14)	$\bar{x}$	64.0	176.2	168.6	138.5	106.3	76.3	59.9	51.0	35.4	18.2	14.3
Length (mm)	SD	28.8	40.2	26.6	12.1	22.1	22.9	11.3	9.1	5.0	2.4	3.8
Unaffected rams (n = 19)	$\bar{x}$	38.1	213.1	184.8	147.1	113.4	88.3	67.6	50.5	36.4	25.3	14.2
Length (mm)	SD	28.9	36.2	20.3	15.9	24.9	19.0	15.8	9.9	10.8	12.2	4.8
t-test		0.0166*	0.0146*	0.0339*	0.0498*	0.2089	0.0709	0.0675	0.4475	0.3882	0.034*	0.4834
Affected rams	$\bar{x}$	72.0	145.4	212.9	255.8	278.9	290.6	294.7	306.0	311.3	312.2	310.7
Circumference (mm)	SD	11.8	20.6	29.5	25.8	17.0	20.6	20.3	17.1	15.1	14.5	11.9
Unaffected rams	$\bar{x}$	71.8	158.3	228.8	272.3	293.4	305.2	312.2	313.6	313.7	310.3	305.8
Circumference (mm)	SD	11.6	17.4	21.2	17.4	13.1	17.8	16.8	17.4	17.8	16.5	19.9
t-test		0.4825	0.0385*	0.0546*	0.0396*	0.0424*	0.0349*	0.0142*	0.1407	0.3825	0.4039	0.3326

* = significant at $P < 0.05$.

the 7th yr, when the horn circumference of unaffected rams was 31.2 cm and 29.5 cm of affected rams.

TABLE 5. Sex specific prevalence of lumpy jaw in North American wild sheep.

Subspecies	Location	Sex	Number of mandibles	Prevalence	Reference
Ovis dalli dalli	Denali National Park, Alaska, USA	♂	367	26.7%	Murie, 1944
	63°40′N, 150°30′W*	♀	304	34.5%	
Ovis dalli dalli	Kluane National Park, Yukon, Canada	♂	49	47.9%	Hoefs
	61°00′N, 138°40′W*	♀	33	75.8%	Unpublished
Ovis canadensis canadensis	Alberta, Canada	♂	96	10.4%	Alberta Government
	51°30′N, 116°00′W*	♀	315	13.1%	Unpublished
Ovis canadensis nelsoni	Desert Game Range, Nevada, USA	♂	191	9.4%	Alfred and Bradley, 1965
	36°40′N, 115°30′W*	♀	118	33.9%	

* Coordinates refer to the centre of a study location.

DISCUSSION

Signs and pathology of lumpy jaw

Lumpy jaw is generally considered a mandibular disease seen in domestic cattle and sheep and in wildlife species such as elk and pronghorn antelope (Murie, 1944; Allred and Bradley, 1965). Occasionally, the disease affects the maxilla, palatine bone and turbinates (Howe, 1981). It is caused by the bacterium *Actinomyces bovis*. The disease generally results in bony proliferations as a response to inflammation and consists of thin trabeculae, granulomatous tissue, and coalescing areas of liquefaction necrosis. Granulomatous tissues often have fistulous tracts or sinuses to the exterior of the mandible and may result in a proliferation of the bone (Glaze et al., 1981). So-called "sulfur granules" have also been described in lumpy jaw infections caused by *Actinomyces* spp. (Heimer et al., 1982). However, most investigations of lumpy jaw in North American wild sheep have failed to isolate *Actinomyces,* spp. and this has led to the assumption that it is not a significant pathogen (Neiland, 1972; Heimer et al., 1982; Schwantje, 1988). However, Cowan (1943, 1944, 1951) found lumpy jaw to be common in the bighorn sheep of Banff and Jasper National Parks (Alberta, Canada) and states, "cultures taken from the jaws of bighorns in Jasper Park have been tentatively identified by Dr. D. C. B. Duff of the University of British Columbia's, Department of Bacteriology and Preventative Medicine as *Actinomyces bovis.*" Later Cowan (1944) revised his position as to the specificity of *Actinomyces* by stating . . . "for present purposes the organism will be referred to as *Actinomyces israeli* as cultures from jaws, lungs and feet abscesses all yielded this species" (Cowan 1951). The pathogen most frequently cultured from infected mandibles of wild sheep with lumpy jaw was *Arcanobacterium py-*

ogenes (Neiland, 1972; Glaze et al., 1982; Heimer et al., 1982). Also identified, but less common was *Fusobacterium necrophorum* (Neiland, 1972). Neiland (1972) obtained samples from a draining abscess of a severe case of lumpy jaw from a live Dall's ewe held in captivity. When exudates were submitted to L. George (Center for Disease Control, Atlanta, Georgia, USA) the only pathogens isolated were *Streptococcus faecium* and *Streptococcus sangius.* When the ewe later died of pneumonia her mandibles were sent to CDC and *Arcanobacterium pyogenes* and *Fusobacterium necrophorum* were isolated from lesions. While there are similarities in signs of the various etiologic agents such as enlarged, lumpy mandibles and associated dental problems, sulfur granules have only been described for *Actinomyces* spp. (Heimer et al., 1982).

Lumpy jaw is believed to result from abnormal wearing of teeth, which leads to drifting and malalignment of the tooth arcade (Glaze et al., 1982). Forage and mineral matter become wedged and compacted between adjacent teeth, causing trauma to the gingiva and periodontia. Coarse and sharp forage items such as the awns of *Stipa* spp. or *Hordeum* spp. or the needles of *Picea* spp. or *Juniperus* spp. are particularly harmful in this context (Hoefs and Cowan, 1979). Secondary bacterial infection may follow the oral trauma. These bacteria are common occupants of the oral cavity and under normal conditions are not pathogenic, but become so when gaining entry into the soft tissue and bone. Loosened, displaced or lost teeth and focal osteonecrosis of the mandible, with or without fistulation may follow. Abnormal wear has been documented primarily on the premolar 3, molar 1 and molar 2 cheek teeth (Glaze et al., 1981; Barichello et al., 1989).

Predisposing factors contributing to the malalignment of the tooth arcade are thought to result from mastication of coarse or heavily loess-covered vegetation (Egorov, 1967; Hoefs and Cowan, 1979; Glaze et al., 1982), defective tooth growth caused by micronutrient or mineral deficiencies (Hungerford, 1975; Orr, 1979) and injuries suffered in fighting (Uhlenhaut and Stubbe, 1980). Green (1949) claimed that lumpy jaw is a significant mortality factor in bighorn sheep in Banff National Park (Alberta), where the bacterium is thought to be transmitted at mineral licks and water holes. We do not share the opinion that lumpy jaw is spread from one animal to another. Even if *Arcanobacterium* spp. were the causative agent, it is a common bacterium which occurs naturally within the oral cavity of wild sheep (Stableforth and Galloway, 1959). Occasionally it becomes pathogenic and precipitates lumpy jaw, when it infects soft tissue.

Prevalence and geographic distribution of lumpy jaw and evolutionary implications

Lumpy jaw appears to be a problem primarily of New World wild sheep. It is rare or absent in the wild sheep of Asia and Europe (Table 1). The reason for this is unknown.

We investigated the possibility of age of a population, in a long-term, evolutionary context, influencing susceptibility to lumpy jaw. The Yukon Territory is suitable for such an assessment, since it is inhabited by sheep populations of varying evolutionary ages. Northern and central Yukon, including the Ogilvie, Wernecke, and British Mountains, were part of the Beringia Refugium (Denton and Hughes, 1981). Populations inhabiting this area can be expected to be very old, more than 13,000 yr and perhaps as old as 100,000 yr (Geist, 1971). When the Wisconsin glaciation came to a close 12,000 to 13,000 yr ago, the ice retreated exposing new potential habitats that could gradually be colonized by sheep as vegetation suitable for grazing became established. About 7,000 yr ago most of the mountain ranges in the Yukon presently occupied by sheep had become exposed. These include the Ruby Range and the Pelly, Hess, and Logan Mountains. Only high elevation areas in the southwest

Yukon, such as the Coast Mountains and the Kluane Ranges became exposed more recently (Denton and Hughes, 1981). These areas are still characterized by extensive mountain glaciation, and the process of glacial retreat, habitat development and colonization by sheep is ongoing. The division of the Yukon into game management zones allowed an allocation of sheep ranges according to their glacial history. We have examined lumpy jaw data from the Yukon (Barichello et al., 1989) accordingly. Yukon's oldest sheep populations, those inhabiting the former glacial refugium, have a moderate prevalence of lumpy jaw with 23.5% (n = 200). The youngest populations, occupying areas recently glaciated, have a high rate of 53.4% (n = 268). Populations in habitats that came into being between 13,000 and 70,00 yr ago have a prevalence of 36.3% (n = 438). Information from Alaska supports this theory. No data are available about sheep populations inhabiting the Beringia Refugium. Prevalences of lumpy jaw were low to moderate in Dry Creek (26%), Sheep Creek (12%), and Denali National Park (25.7%) herds, which occupy areas in the northern Alaska Range, close to the unglaciated area. These regions were colonized by sheep long before the Kenai Peninsula became available, whose sheep have a prevalence of lumpy jaw of 40% (Table 2). The range of the Stone's sheep of northern British Columbia and adjacent areas of the Yukon was entirely glaciated. It was colonized by sheep moving in from the north (Geist, 1971). As a subspecies, Stone's sheep are more recent in origin than Dall's sheep. In our sample of 198 Stone's sheep mandibles, the prevalence of lumpy jaw was 29.3% (Table 1), with even higher rates reported in specific collections (Table 2).

The bighorns show significant regional differences in their susceptibility to lumpy jaw. It is generally accepted that the Rocky Mountain bighorn (*O canidensis canadensis*) is the most advanced type within this species (Geist, 1971). Based on a sample size of 961, including specimens from many areas, we found an overall prevalence of 12.1%. However there are significant regional differences within this subspecies. Northern populations occupying formerly glaciated areas show a high prevalence of lumpy jaw approaching that of Dall's sheep, while southern populations at the edge of glaciated terrain or in habitats south of it show a low prevalence. Consultations with biologists in Montana, Wyoming, Idaho, Washington and Colorado (USA) reveal that lumpy jaw is rare in the bighorns of those states. In contrast the average rate in the province of Alberta is 12.5% (n = 411). Infection rates as high as 66% have been reported for the Canadian national parks in the Rocky Mountains (Cowan, 1943). Overall the prevalence in other subspecies of *O. canadensis* is lower (Table 1), but high rates have been reported for specific populations of desert sheep. These reports consist mainly of aberrations of the tooth arcade without mandibular osteomyelitis, such as those occupying the Desert Game Range (Nevada, USA) (Allred and Bradley, 1965). Our sample of the desert bighorns included only 79 specimens from the desert sheep of Baja California. None of these were infected.

We provided evidence that in North American sheep populations living in or near formerly glaciated areas an inverse relationship exists between prevalence of lumpy jaw and age of a population in a long-term evolutionary context. We speculate that both extrinsic and intrinsic factors may be responsible. Sheep are a product of the ice age, and new habitats usually came into being when glaciers retreated. Vegetation became established in these newly exposed areas, and subsequently sheep and other animals invaded it and new populations became established. There was as yet no soil development. Coarse material covered the ground and frequent down-glacier winds covered the vegetation with silt (loess). As a result it can be assumed that sheep ingested a relative high amount of mineral matter along with their forage, which led to escalated tooth abrasion and fascilitated entry of pathogens into their oral tissues (Glaze et al., 1982). Geist's (1978) "dispersal theory" may help to explain this relationship by means of intrinsic factors. This theory revolves around the duality of phenotypes that arise at extreme ends of resource availability. Food abundance generates the "dispersal," whereas shortages favor the "maintenance" or "efficiency" phenotypes. The former is characterized by large bodies, large skulls, rapid initial horn growth followed by slow growth in the later years, early sexual maturity, high reproductive rates, but a short life expectancy. By contrast, the maintenance phenotypes are characterized by smaller bodies and skulls, retarded initial horn growth but improved development in later years, delayed sexual maturity, lower productivity, but a longer life expectancy. While Geist (1978) did not address differences in susceptibility to disease between these two types, one can assume that the shorter life expectancy of the "dispersal" type implies less resistance to disease. More recently evolved, new populations are dominated by the "dispersal" type.

Impact of lumpy jaw on wild sheep

Information on the biological significance of lumpy jaw in populations of wild sheep is very limited. However, investigators usually made assumptions about possible implications. Green (1949) concluded, "Actinomycosis is invariably a chronic condition which ultimately results in death from malnutrition and starvation." Cowan (1944) speculated, "it seems then that actinomycosis usually kills by inducing malnutrition." Barichello et al. (1989) stated, ". . . we found no evidence that lumpy jaw infection is debilitating to sheep populations in the Yukon."

Several investigators have provided evidence that lumpy jaw affects primarily mature, older animals (Allred and Bradley, 1965; Stelfox, 1974; Glaze et al., 1982). From his large sample of mandibles from Denali National Park (n = 829), Murie (1944) concluded that lumpy jaw lowers life expectancy because affected sheep are more vulnerable to predation by wolves. This view of a lowered life expectancy is shared by Allred and Bradley (1965) who wrote: "Necrosis and other dental problems must be considered an important limiting factor affecting the ecological life expectancy of a population." Neiland (1972) assumed that lumpy jaw affects individuals and populations in two principal ways: "If extensive malocclusions and/or loss of molars significantly impair mastication of forage, the victims will not be able to efficiently utilize what they eat and will lose condition disproportionally to the prevailing seasonal, nutritional potential of the range they inhabit . . . Another way in which chronic lumpy jaw may seriously impact the victims' welfare is that such abscesses may serve as reservoirs of infections from which other organs may be infected."

Data from the long term investigation of Dall's sheep in Kluane National Park did not indicate that lumpy jaw is a disease primarily affecting older sheep or that it lowers life expectancy. A possible explanation for the sex-specific discrepancy in prevalence of lumpy jaw is the difference in range use strategies between the sexes. Females, particularly when accompanied by young, do not venture far from the security of escape terrain. Rams, on the other hand, do. They accept a higher risk of attack by predators in exchange for access to better forage (Frid, 1994). Forage close to escape terrain is often scarce or overgrazed because of heavy use. Less palatable, coarse plant species may become established at such sites.

Information obtained from the Kluane National Park, Yukon Territory, Canada, points to a negative effect of lumpy jaw on horn development of rams. The data in Table 4 may underestimate the severity of this problem, since it is conceivable that some of the rams with lumpy jaw contracted this disease late in life, and their early horn segments reflected healthy conditions. The length of horn growth in the first year (lamb tip) is usually not considered in comparisons (Bunnell, 1978), since it reflects different degrees of tip wear and damage rather than initial length. It is known that damage to the horn tip or "brooming" is primarily the result of fights between rams (Shackleton and Hutton, 1971; Uhlenhaut und Stubbe, 1980). Since the horn circumferences at the end of the first year were identical in affected and unaffected rams (72 versus 71.8 mm), we conclude that their initial first year's horn lengths were also comparable, and that the differences observed reflect a lower amount of tip damage by affected rams, perhaps because of a more lethargic, indifferent disposition.

There is little or no experimental evidence of negative effects of lumpy jaw on wild sheep. However, sufficient information exists on domestic sheep that documents adverse impact on forage intake, mastication, animal condition, productivity and longevity (Gunn, 1970; Newton and Jackson, 1983). It can be assumed that wild sheep will be similarly affected.

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