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EXPERIMENTAL INFECTIONS OF FREE-RANGING ROCKY MOUNTAIN BIGHORN SHEEP WITH LUNGWORMS (*PROTOSTRONGYLUS* SPP.; NEMATODA: PROTOSTRONGYLIDAE)

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ABSTRACT: Twelve free-ranging Rocky Mountain bighorn lambs (*Ovis canadensis canadensis*), each exposed experimentally to 125–1,000 infective third-stage larvae of *Protostrongylus stilesi* and *P. rushi*, shed significantly more first-stage larvae in their feces than did control lambs, but showed no clinical signs of illness and had equivalent summer and overwinter survival as control lambs. Two adult ewes, each exposed to 925 infective larvae, showed no increase in numbers of first-stage larvae in their feces; both survived at least 14 mo postexposure. Experimentally exposed lambs did not differ from control lambs in numbers of larvae in their feces in the following summer. Three experimental lambs had 313–402 adult *P. stilesi* and 0–97 adult *P. rushi* on necropsy; two control lambs had 255 and 270 *P. stilesi* and no *P. rushi*. The presence of these numbers of lungworms did not appear to be sufficient to precipitate lungworm pneumonia in bighorn lambs under the conditions of this study.

Key words: Bighorn sheep, *Ovis canadensis canadensis*, lungworm-pneumonia complex, *Protostrongylus stilesi*, *Protostrongylus rushi*, experimental infections.

INTRODUCTION

Lung disease appears to play a major role in the population dynamics of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) (Buechner, 1960; Stelfox, 1971; Spraker and Hibler, 1982). Much of this disease appears to be associated with the lungworm-pneumonia complex, an association of nematode lungworms (usually *Protostrongylus stilesi* or *P. rushi*) complicated by bacterial or viral pneumonia (references above).

Spraker and Hibler (1982) distinguished three patterns of mortality associated with the lungworm-pneumonia complex: Type 1, a mass mortality that affects all sex and age groups; Type 2, mortality of lambs in the summer that follows a mass mortality; and Type 3, summer mortality of lambs at other times. Type 1 mortalities are generally regarded as being stress-induced (Spraker et al., 1984), and have many of the characteristics of epidemics due to bacteria (Onderka and Wishart, 1984) or viruses (Parks et al., 1972); lungworms appear to play an unimportant proximal role, but may play an important ultimate role as a predisposing factor. Type 2 mortalities appear to be stress-related, as evidenced by atrophied thymus glands; lungworms do not appear to play a significant role. Type 3 mortalities appear to be due to an extensive suppurative verminous bronchopneumonia, complicated by viral, bacterial or mycoplasmal infections. This type of mortality seems to be intimately associated with the production of larvae by lungworms acquired by transplacental transmission (Hibler et al., 1972, 1974; Spraker, 1979). Affected lambs "have frequent paroxysms of coughing; rough, yellow, shaggy hair coats; . . . are small in size and light in body weight compared to healthy lambs; . . . seldom frolic and generally lag behind the herd during any activity" (Hibler et al., 1982, p. 211).

Both transplacental transmission of lungworms (Gates and Samuel, 1977) and late summer mortality of lambs with the clinical signs described by Hibler et al. (1982) are known in bighorn herds in Alberta (Horejsi, 1976; Festa-Bianchet and

Samson, 1984), so the Hibler/Spraker hypothesis that mortality is due to extensive prenatal infection may apply. However, the Type 3 mortality pattern is also consistent with the hypothesis that such mortality is due to inadequate immune responses on the part of the lamb due to stress or malnutrition following early weaning by a ewe in poor condition. The two hypotheses are not mutually exclusive and could both be involved in a complex etiology. However, an initial assessment of the validity of the two hypotheses could be provided by experimental infections of lambs in a herd in which the animals were in good condition, with no Type 3 mortalities at the time. Because it is currently impossible to manipulate prenatal infections in wild, free-ranging bighorns, we assessed the two hypotheses by experimentally exposing lambs as young as possible.

In this paper, we report that young lambs experimentally exposed to infective larvae of *Protostrongylus* spp. shed large numbers of first-stage larvae (L_1's) in their feces, but showed none of the signs associated with Type 3 mortality, had excellent summer and over-winter survival, and shed normal numbers of L_1's in their feces in the following summer.

MATERIALS AND METHODS

Study herd

The Ram Mountain herd inhabits the southernmost end of the Brazeau Range (52°25′N, 115°45′W) in Alberta, and is isolated from other bighorn herds by surrounding conifer-covered foothills and the North Saskatchewan River. The range varies in elevation from 1,082 to 2,173 m, with treeline at about 1,800 m. This herd has been studied by the Alberta Fish and Wildlife Division since 1971 (summarized in Jorgenson and Wishart, 1987); this experiment was done as a part of that study. The herd was stabilized (by ram hunting and experimental ewe removals) at about 100 animals from 1973 through 1981, then allowed to expand, reaching 132 in 1984. It was a relatively young herd, with a mean of 69% of the animals <4 yr old. From 1971 through 1984, there was a mean of 29 reproductively active ewes (including three yearlings), which produced a mean of 23 lambs per year. From 1975 through 1984, overwinter survival rates averaged 80% for lambs, 93% for ewes and 84% for rams.

The Ram Mountain herd has been rated as high quality (using the criteria of Geist, 1971) in terms of productivity, survival, and life expectancy, but not in terms of final body or horn size. By 1985, when herd size had reached 142 animals, indications of decay in herd quality were apparent. The age structure became older (59% <4 yr), overwinter lamb survival decreased to 72% (50% of males), productivity was reduced (the proportion of barren ewes doubled, only one yearling produced a lamb), and growth increments of horns were smaller. Therefore, our field experiments began during a period of high herd quality (1982), but finished during a period of declining quality (1984).

Over 95% of all animals were marked individually by Fish and Wildlife personnel, so that most fecal samples could be associated with a specific individual. Most animals (including all those examined at least twice) harbored lungworms. Numbers of larvae in the feces (larvae per gram of dry feces, LPG) showed the typical seasonal cycle (Uhazy et al., 1973), averaging 94 LPG (range = 0–1,879) in June and July and 743 LPG (range = 20–2,536) in late winter over the period 1977–1984. *Protostrongylus stilesi* and *P. rushi* are both present (Uhazy et al., 1973) in this herd.

Experimental protocol

Over a period of 3 yr (1982–1984), third-stage larvae (L_3's) of *Protostrongylus* spp. (*P. stilesi* and *P. rushi*) were administered orally to 12 lambs and two mature ewes (Table 1). Ewes with lambs were captured, as soon after lambing as possible, in a corral trap, using salt as bait. In this herd, lambs are born over a 3-wk period, with most lambs born the third week of May; lambs are 2 to 3 wk old when they first leave the lambing grounds (J. Jorgenson, pers. obs.). Colored identification streamers and numbered tags were affixed to the ears of any unmarked sheep. Small, solar-powered radio transmitters (Wildlife Materials Inc., Carbondale, Illinois 62901, USA) were attached to 10 mm braided nylon rope and loosely fastened around the neck of some lambs, including those experimentally infected. (All lambs were captured the following year, so the problem of collar expansion was not an issue.) Fecal samples were taken from each lamb.

Protostrongylus spp. L_3's were obtained from

TABLE 1. Rocky Mountain bighorn sheep exposed to experimental infections with *Protostrongylus* spp., with data on numbers of first stage protostrongylid larvae shed per gram of dried feces (LPG).

Sheep number	Date	Age (wk)	Dose (number of L3's)	Before 20 days PE[a] Maximum LPG	After 30 days PE[b] Maximum LPG	After 30 days PE[b] Mean LPG	After 30 days PE[b] >600 LPG[c]
1	10 June 1982	2–3	125–150	0 (1)[d]	1,090	812	2/3
2	10 June 1982	2–3	125–150	0 (1)	800	420	1/2
3	10 June 1982	2–3	125–150	20 (2)	693	693	1/1
4	21 August 1982	12–13	125–150	251 (3)	150	150	0/1
5	21 August 1982	12–13	125–150	644 (1)	1,102	1,102	1/1
Controls (18)			0	21 (3/9)[e]	874	74	1/32
6	17 June 1983	3–4	1,000	0 (1)	2,774	233	3/10
7	17 June 1983	3–4	1,000	0 (1)	5,402	713	4/8
8	22 June 1983	4–5	1,000	0 (1)	3,707	1,636	9/10
Controls (33)			0	—	977	104	1/44
9	11 June 1984	2–3	1,000	0 (1)	—		
10	11 June 1984	2–3	1,000	0 (2)	—		
11	17 June 1984	3–4	1,000	250 (2)	2,807	235	4/7
12	17 June 1984	3–4	1,000	1,065 (3)	1,938	572	7/11
Controls (31)			0	833 (11/20)	1,802	124	5/20
A	30 June 1984	adult	1,000	83 (4)	—	—	—
B	30 June 1984	adult	1,000	33 (2)	172	77	0/10
Controls (15)		adult	0	338 (20/21)	141	14	0/19

[a] Controls sampled on or before 30 June 1982, 7 July 1983 or 1984.
[b] Controls sampled on or after 10 July 1982, 17 July 1983 or 1984.
[c] 600 is mean + 1 standard deviation (control lambs, July–September, all years combined).
[d] Number of samples.
[e] Number positive/number of samples.

laboratory infections in *Vallonia pulchella* as outlined by Samson and Holmes (1985). The darkened cuticle of infective L_3's can be seen in the intact foot of an infected snail. The number of infective L_3's in the foot was counted, the foot was severed and placed in saline, and snails containing the desired numbers of larvae were drawn up into a syringe and delivered orally, via a plastic tube, to the experimental lambs. The syringe was rinsed and the rinse water also delivered orally to the lambs.

Control lambs were handled in exactly the same manner, except that not all were radio-collared. In 1982, all were given worm-free saline (as above), but in 1983 and 1984, they were not.

Movements of the experimental and control lambs were monitored throughout each summer. Fecal samples were collected as often as possible by locating each lamb, observing it with a ×45 spotting scope until it defecated, and keeping the fecal pile under observation through the scope until an assistant collected the fresh feces. The behavior (play, resting time, appearance of any of the signs described for sick lambs) of experimental and control lambs was noted and compared subjectively.

Heavy snows prevented access to the mountain after October, but helicopter surveys were conducted in November 1982 and January 1983 to locate radio-collared lambs and check for animals lagging behind the herd or showing any of the other clinical signs of sick lambs.

Numbers of lungworm larvae per gram dried feces were determined by the methods of Samuel and Gray (1982). Because counts of lungworm larvae show a lognormal distribution (Uhazy et al., 1973), all counts were transformed to $\ln(x + 1)$ before performing statistical analyses. To minimize seasonal variation, only samples from June through September were used. Statistical analyses, including Satterthwaite's approximation to correct for disparate sample sizes, are from Sokal and Rohlf (1981), using programs from the package BIOM obtained from F. J. Rohlf (Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, USA).

Lambs to be examined for lungworms were shot and returned to the Animal Health Divi-

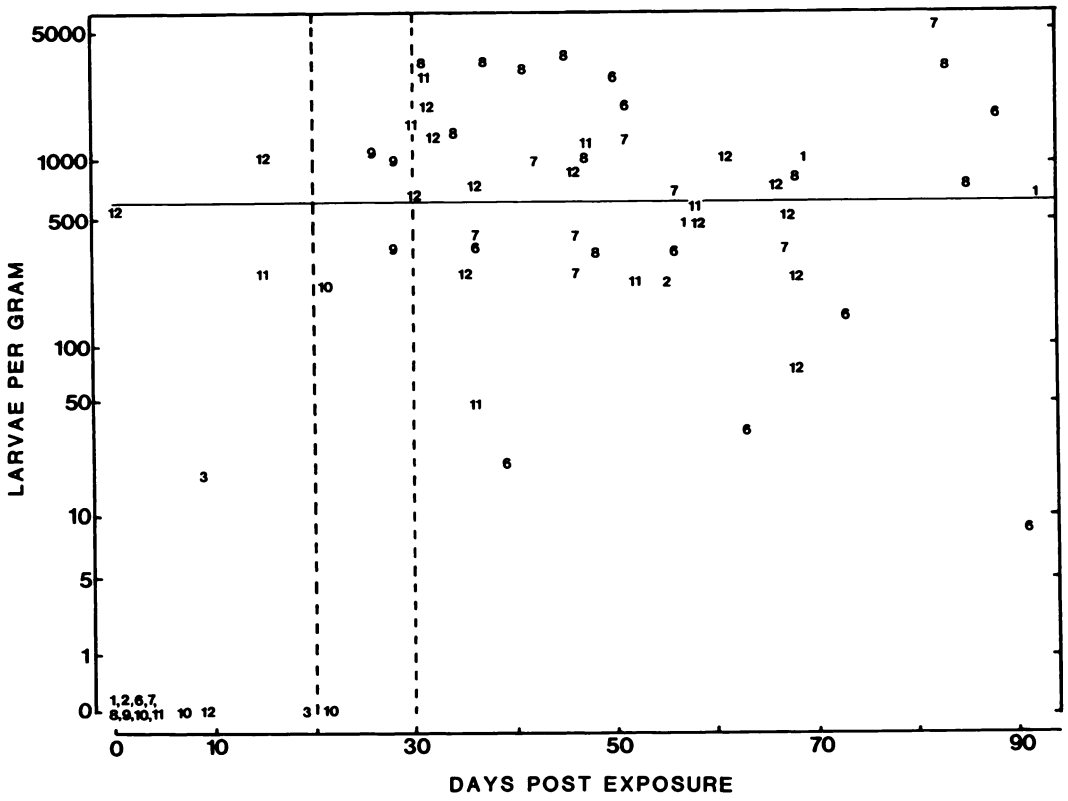

FIGURE 1. Number of *Protostrongylus* spp. larvae per gram dried feces from Rocky Mountain bighorn lambs experimentally infected in June (1982–1984) as a function of days after exposure. Numbers indicate the lamb from which the sample was taken (see Table 1 for additional data). The horizontal line indicates the mean plus one standard deviation of data from control lambs (using ln(x + 1) transformed data). The two vertical broken lines encompass the probable prepatent period. Positive values to the left of the first line are indicative of prenatal infections, values to the right of the line at 30 days post exposure represent (at least in part) the results of the experimental infections. See text for discussion.

sion, Alberta Agriculture, Edmonton, where they were necropsied. Lung and tonsil swabs were cultured for bacteria; no examinations for viruses were done. The lungs were frozen, then later thawed, divided into small pieces, and completely teased apart to recover adult and larval lungworms.

RESULTS

Data on numbers of larvae in the feces of 10 lambs exposed in early to mid June (years combined) are shown in Figure 1. Most of the samples taken through 20 days postexposure (PE) were negative; none of the samples taken 30 or more days PE was negative. The latter time approximates the prepatent period estimated by Spraker (1979). We therefore treat positive counts obtained prior to 20 days PE as naturally acquired (presumably transplacental) infections, and those taken after 30 days PE as experimental infections (at least in part). Using this interpretation, at least three of these 10 experimental lambs (and 18 of 34 control lambs) were infected naturally, probably transplacentally, before exposure (Table 1). In addition, the two lambs exposed in August were shedding L_1's when exposed. Thus, at least some of the worms in our experimental lambs were derived from natural infections. Nonetheless, the data indicated that the experimental infections were successful.

TABLE 2. Nested ANOVA analysis of the number of first stage protostrongylid larvae per gram of dried feces (LPG) shed by experimental versus control Rocky Mountain bighorn lambs. Values for degrees of freedom (DF) and mean squares (MS) are adjusted values, using Satterthwaite's approximation, to correct for unequal sample sizes. See Sokal and Rohlf (1981) for details.

Source of variation	df	MS	F	Percent of variance
Years	2	5.765	0.141[a]	0.0
Experimentals vs. controls (within years)	2.4	40.792	5.201[b]	29.3
Sheep (within groups)	39.9	7.844	5.501[c]	33.6
Samples (within sheep)	79	1.426		37.2

[a] Not significant, $P > 0.05$.
[b] Significant at $P < 0.01$.
[c] Significant at $P < 0.001$.

Data (LPG, samples taken at least 30 days PE) from the experimental lambs, plus data taken over the same time periods from the 82 control lambs, were analyzed using a nested analysis of variance, with experimental and control groups nested within years, and all available samples from the same lamb treated as replicates. The results (Table 2) indicated that there was considerable variation in numbers of larvae from different samples from the same lamb, considerable variation among lambs, and no significant variation among years. Despite the variation in the data, the experimental lambs did have significantly higher LPG than controls. In addition, lambs given 1,000 larvae had considerably higher maximum LPG's (1,900–5,400) than did lambs given 125–150 larvae (150–1,100) (Table 1).

Experimental lambs from 1982 and 1983 were sampled also the following summer, as yearlings. A nested analysis of variance indicated that, given the variation among samples from the same yearling, there was no significant variation among yearlings ($F = 0.998$, $P > 0.25$), nor between experimental and control animals ($F = 1.981$, $P > 0.10$).

Only one of the two ewes fed larvae in 1984 could be sampled during that same summer. A nested analysis of variance indicated that the numbers of larvae shed by that ewe did not differ from controls ($F = 0.955$, $P > 0.25$). In a limited number of samples taken in October, experimental ewes (two samples from each) had higher LPG's than during the summer, but no higher than three control ewes (single sample each).

In 1984, five lambs, three experimentals and two controls, were collected and examined for nematodes in the lungs. Details of dates of exposure and examination are given in Table 3. All harbored at least 250 adult or L_4 *P. stilesi*, the experimentals all harbored more than the controls, and two of three experimentals (but neither of the controls) also harbored adult or L_4 *P. rushi* (Table 3). All had some gravid *P. stilesi*, and all lambs >3 wk of age had first stage larvae in the lungs or feces. Details on the pathology and distributions of the worms in the lungs of these animals will be reported elsewhere. However, none of the lungs showed the severe lesions described by Spraker (1979). Potentially pathogenic bacteria were isolated from the tonsils of all five lambs; a non-hemolytic *Pasteurella hemolytica* type T, the type associated with extensive mortality in bighorns in southwestern Alberta in the early 1980's (Onderka and Wishart, 1984), was found in three of the lambs (Table 3).

None of the experimental lambs showed any of the signs of disease described by Hibler et al. (1982). None had a persistent cough, a scruffy hair coat, or showed any obvious differences in play or time spent resting. The three experimental lambs in 1982 were the same size (22.8 ± 1.0 kg) as controls (24.6 ± 3.8 kg, $n = 11$) when weighed in late August. In contrast, a control lamb that was abandoned by its dam in early June 1982, when it was about 3

TABLE 3. Adult and fourth stage larvae of protostrongylid nematodes recovered from the lungs of necropsied Rocky Mountain bighorn lambs. Sheep identification numbers, in column one, are those in Table 1.

Sheep number	Date infected	Date examined	Age (wk)	*Protostrongylus* *stilesi* Total	*Protostrongylus* *stilesi* Gravid females	*Protostrongylus* *rushi* Total	*Protostrongylus* *rushi* Gravid females	Total
9	11 June	9 July	7	313	92	3	0	316[a]
10	11 June	2 July	6	402	135	97	11	499[a,b,c]
11	17 June	14 Aug.	12	402	148	0	0	402[b]
Control		11 June	3	255	11	0	0	255[a]
Control		9 July	7	270	113	0	0	270[d]

[a] *Pasteurella hemolytica* type T isolated from tonsils.
[b] *Pasteurella hemolytica* type A isolated from tonsils.
[c] Corynebacteria isolated from tonsils.
[d] Beta-hemolytic *Escherichia coli* isolated from tonsils.

wk old, was visually smaller than others, did cough, had a scruffy coat, and was passing 874 LPG in August. The effects of lungworms in this animal were probably complicated by the effects of malnutrition.

The experimental lambs survived at least as well as controls (Table 4). All these lambs survived through the autumn, and only one died over the first winter (lamb 12 in Table 1, which was shedding over 500 LPG when exposed). The abandoned lamb mentioned above also died over the first winter. Both experimental adult ewes survived overwinter, as did their lambs. However, one ewe lost its lamb postpartum in 1985.

TABLE 4. Survival of experimental Rocky Mountain bighorn sheep, exposed as lambs, and controls, 1982–1984. Animals collected are not included in the totals.

Year	Class	Number	Survival after 1 yr	Survival after 2 yr	Survival after 3 yr
1982	(Experimentals)	5	5	4	3
	(Controls)	21	17	13	13
1983	(Experimentals)	3	3	2	
	(Controls)	23	18	14	
1984	(Experimentals)	1	0		
	(Controls)	24	18		
Total	(Experimentals)		8/9 89%	6/8 75%	3/5 60%
	(Controls)		53/68 78%	27/44 61%	13/21 62%

DISCUSSION

Our data, like those of Forrester and Senger (1964), showed considerable variation in the numbers of *Protostrongylus* spp. larvae among samples taken from the same animal. Nonetheless, the consistently high maximum LPG in experimental lambs exposed in June, the higher maxima in those exposed to 1,000 larvae, and the significantly higher mean LPG in experimental lambs, all indicated that the experimental infections were successful (i.e., did result in elevated numbers of adult lungworms). The limited data on experimental infections in ewes provided no evidence of successful reinfection.

The data on numbers of worms in the lungs of experimental and control lambs are difficult to interpret. The only experimental lamb collected late in the summer (lamb 11 in Table 3) had a maximum LPG (2,807) within the range (1,938–5,402) of other experimental lambs given 1,000 L_3's. In addition, each of the three experimental lambs had more *P. stilesi* than either of the controls, and *P. rushi* was present in two of the experimental lambs but not in

either of the controls. Again, the data indicate that the experimental infections did increase the numbers of lungworms, but are inadequate to determine by how much.

Hibler et al. (1982, p. 210) reported that "Lambs born in sheep populations where verminous pneumonia is responsible for severe lamb mortality frequently are infected with 100 to 500 larvae. The exact number necessary to predispose lambs to fatal verminous pneumonia is unknown, but 100 probably is sufficient." Despite the large number of lungworms (in both experimentals and controls), the presence of large numbers of first stage larvae in the lungs, and the presence of potentially pathogenic bacteria, the lambs necropsied in this study did not have the severe lung lesions described by Spraker (1979).

These data, plus those on survival of experimental lambs, indicate that mixed transplacental and early oral infection with substantial numbers of lungworms (up to approximately 400 adult and L_4 *P. stilesi*, including 130–140 gravid females) was not sufficient to precipitate a lungworm pneumonia adequate to kill (or even cause clinical signs in) bighorn lambs that were in good condition. In turn, this conclusion suggests that these numbers of lungworms are not sufficient to produce the Type 3 mortality of Spraker and Hibler (1982), even in the presence of potentially pathogenic bacteria. It is possible that a larger number of lungworms, or even the same number of lungworms acquired transplacentally, could produce Type 3 mortality. It is also possible that Type 3 mortality requires the presence of a specific secondary invader not present in the Ram Mountain herd.

However, it appears more likely that Type 3 mortality, like Types 1 and 2, is dependent on reduced resistance of the lambs due to stress or malnutrition. The clinical signs of lungworm pneumonia shown by the abandoned lamb in this study, and its subsequent overwinter death, support such a conclusion. Additional support is provided by the correlations among high late-winter LPG of ewes, reduced suckling times, and mortality of their lambs the subsequent summer and fall found by Festa-Bianchet and Samson (1984).

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