Numbers of lungworm larvae in feces of bighorn sheep: yearly changes, influence of host sex, and effects on host survival

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The number of *Protostrongylus* spp. first-stage larvae in the feces of marked bighorn sheep (*Ovis canadensis*) was monitored from 1981 to 1988 in southwestern Alberta. Prevalence of infection was 100%. Counts were not correlated with spring precipitation, winter temperature, or number of female sheep in the study population. Percent lamb survival and average counts were correlated only when years affected by the occurrence of a pneumonia epizootic were excluded. In the years before the epizootic, but not afterwards, lambs born to females with high larval counts were less likely to survive to weaning or to 1 year of age than lambs born to females with low counts. Fecal larval counts from the same female in successive years were weakly correlated, and tended to change towards the mean for all females. Counts were affected by host reproduction but not by seasonal migration, and did not affect host survival. Among lambs and yearlings, males had higher counts than females. Lambs had higher counts than adult females. There were no age-specific differences among adult females. The larval count from female lambs was correlated with that from their mother but not that from male lambs. Heart girth of female lambs was correlated with their larval count and that of their mother. I suggest that larval counts are affected by infection intensity and body condition, do not predict pneumonia epizootics, and have limited reliability as an index of herd health.

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Les larves de premier stade de *Protostrongylus* spp. ont été dénombrées dans les fèces de Mouflons d'Amérique (*Ovis canadensis*) marqués du sud-ouest de l'Alberta, de 1981 à 1988. Tous les mouflons étaient infectés. Il n'y avait pas de corrélation entre le nombre de parasites et les précipitations de printemps, la température durant l'hiver ou le nombre de femelles dans la population étudiée. Il y avait corrélation entre la survie des agneaux, exprimée en pourcentage, et le nombre moyen de parasites seulement après avoir éliminé des analyses les années où la population était affectée d'une épizootie de pneumonie. Au cours des années précédant l'épizootie, mais pas après, les agneaux issus de femelles à infections graves avaient moins de chance de survivre jusqu'au sevrage ou jusqu'à l'âge de 1 an que les agneaux issus de femelles moins infectées. Il n'y avait qu'une faible corrélation entre les densités de parasites dans les fèces d'une même femelle au cours d'années successives et le nombre de parasites dans les fèces avait tendance à se rapprocher de plus en plus de la moyenne chaque année chez toutes les femelles. Le nombre de parasites était affecté par la reproduction des hôtes, mais pas par leur migration saisonnière, mais n'affectait pas la survie des hôtes. Chez les agneaux et les jeunes de 1 an, les mâles portaient un plus grand nombre de parasites que les femelles. Les agneaux avaient plus de parasites que les femelles adultes. Il n'y avait pas de différences dues à l'âge entre les femelles adultes. Le nombre de larves chez les agneaux était en corrélation avec le nombre de parasites de la mère seulement chez les agneaux femelles. Le périmètre du coeur des agneaux femelles était en corrélation avec le nombre de leurs parasites et le nombre de parasites de leur mère. Il faut conclure que la densité des larves est fonction de la gravité des infections et de la condition physique des hôtes, qu'elle ne permet pas de prédire les épizooties de pneumonie et que sa valeur comme indicateur de la santé d'un troupeau est discutable.

[Traduit par la rédaction]

Introduction

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) are parasitized by two species of nematode lungworms, *Protostrongylus stilesi* in the lung parenchyma and *P. rushi* in the bronchi and bronchioles (Uhazy et al. 1973). Lungworms have been implicated in pneumonia epizootics, which cause high mortality (Marsh 1938; Stelfox 1971; Onderka and Wishart 1984). Despite frequent use of the term lungworm–pneumonia complex, however, there is no firm evidence that lungworms cause pneumonia (Samson et al. 1987), except possibly in lambs infected transplacentally in some populations (Spraker 1979).

The potential effects of lungworm infection upon survival and reproductive success of bighorn sheep are of interest from theoretical and applied viewpoints, yet little information is available about them. Ideally, one would want information on infection intensity and related pathology, but for free-ranging wild animals collection of this information requires killing the host. Individual fecal larval counts may be a useful surrogate for studies of the relationship between wild animals and their parasites.

Forrester and Littel (1976) claimed that spring precipitation influenced lungworm infection by affecting the abundance of the snail intermediate hosts. Wishart et al. (1980) suggested that the timing of return to the winter range would affect lungworm infection. They believed that snails would be less abundant in the high-elevation summer range, and that sheep that returned early (before hard frosts) may be reinfected. Stelfox (1976) suggested that counts of first-stage larvae in sheep feces were correlated with density and weather, with high counts following cold winters or occurring in high-density populations where forage was overexploited.

Here I summarize the results of an 8-year investigation of lungworm infection in bighorn sheep, relating individual counts of first-stage larvae in sheep feces and year-to-year changes in counts to individual, population, and environmental variables. I have already shown that larval counts vary with reproductive effort (Festa-Bianchet 1989*a*), and that they correlate with maternal behavior (Festa-Bianchet 1988*a*). The goals of this study were (*i*) to compare larval counts of the same individual in successive years; (*ii*) to analyze the effects of weather,

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population density, timing of seasonal migration, age, and sex upon larval counts; and (*iii*) to determine if individual larval counts are correlated with survival, body size, and reproductive success. I also examined the possibility of a maternal effect on larval counts by comparing the counts from mothers and offspring.

Long-term studies of individuals allow the collection of data necessary to understand any effects of changes in population density, host sex and age, and weather upon larval counts. This study also assessed the usefulness of larval counts as a measure of population "health" and as predictors of pneumonia epizootics.

Materials and methods

The study population wintered in the Sheep River Wildlife Sanctuary in southwestern Alberta (details in Festa-Bianchet 1986). Data reported in this paper were collected between 1981 and 1989. Bighorn sheep were captured with a corral trap or a tranquilizer gun (Festa-Bianchet and Jorgenson 1985), measured, and marked with Allflex ear tags. Heart girth and horn length of lambs caught between August 20 and November 30 were adjusted to October 1 (the approximate date of weaning, see Festa-Bianchet 1988*a*), using sex-specific regressions. Fecal samples, collected after watching marked sheep until they defecated, were stored in paper bags, dried, and examined for larvae by means of the Baermann technique (Samuel and Gray 1982). Unfortunately, this analysis does not distinguish between species of *Protostrongylus*.

Most analyses were limited to fecal samples collected in March and April, because lungworm larval counts peak in late winter and early spring (Uhazy et al. 1973). Limiting analysis to March and April samples avoided the confounding effects of seasonal fluctuations. February samples were included for lambs, to increase sample size. No consistent differences were found between February, March, and April samples. Overall, 2376 samples were collected from 155 bighorns between 1981 and 1988. Included were 137 sheep sampled in March–April (1198 samples).

The Baermann analysis estimates the number of first-stage larvae per gram of dry feces (LPG). The LPG values are positively skewed, and Uhazy et al. (1973) applied a natural logarithmic transformation to them. In this study, a natural log transformation resulted in significant negative skew. A square-root transformation approximated a normal distribution, therefore LPG values were square-root transformed. Transformed counts of all samples collected from each sheep each year were averaged, and this average (tLPG) was used for analyses. Parametric statistics with two-tailed probability levels were used unless otherwise specified. Sex (male/female), survival (yes/no), and pregnancy (yes/no) were coded as dummy variables for multiple regressions (Kerlinger and Pedhazur 1973). Proportional data were arcsine transformed (Sokal and Rohlf 1981). The SPSS package (SPSS Inc. 1983) was used for all analyses. Means are reported ±1 standard error.

Previously (Festa-Bianchet 1988*a*, 1989*a*) I eliminated subsets of data to reduce repeated sampling of the same individual. If samples from the same individual are closely correlated, and repeated observations make up a large proportion of the data set, distortions of estimated probability values may result (Machlis et al. 1985). I used all data because of the weak correlation between tLPG values from the same sheep in different years (see Results) and because analyses in which each individual was included once gave the same results. No female was sampled in more than 8 years (making up 2.2% of the total sample), and on average 3.7 years of data were available for each female ($N = 102$). I indicate throughout whether N refers to individuals or sheep-years.

Methods used to age individuals, determine population size, and monitor reproductive success are described elsewhere (Festa-Bianchet 1986, 1988*b*, 1989*a*). Females referred to as pregnant are those that lactated later in the year. Weather data were obtained from Environment Canada for the High River station, approximately 40 km southeast of the study area. As fecal samples were collected in March–April, sheep referred to as lambs were 9–11 months old, yearlings were 21–23 months old, and so on.

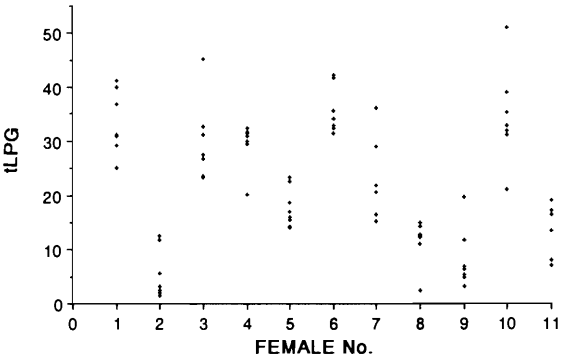

FIG. 1. Square-root transformed counts of *Protostrongylus* spp. first-stage larvae (tLPG) in fecal samples collected in southwestern Alberta from adult female bighorn sheep during one March–April period.

TABLE 1. Average square-root transformed fecal counts of *Protostrongylus* spp. first-stage larvae from adult female bighorn sheep in southwestern Alberta, March–April 1981–1988

Year	*N*	Average	SE
1981	13	19.15	2.12
1982	24	24.50	1.87
1983	24	21.69	1.82
1984	46	21.15	1.57
1985	50	22.67	1.17
1986	31	20.47	1.57
1987	34	29.91	0.96
1988	37	24.80	1.00

NOTE: *N*, number of females sampled each year.

Results

Prevalence of *Protostrongylus* spp. infection was 100% ($N = 155$ sheep). Although 1.2% of samples were negative, larvae were found in some samples from all sheep. Only nine samples (0.4%) exceeded 3200 LPG (56.57 transformed count, tLPG), up to 8601 LPG (92.74 tLPG) from a female in poor condition that died within 2 months. Samples collected from the same individual over any one March–April period showed considerable variation (Fig. 1).

Average tLPG of adult females was similar in all years except 1987 ($F_{[7,261]} = 4.580$, $P = 0.0001$). Mean tLPG in 1987 was greater than in 1981, 1983, 1984, and 1986 according to Scheffé multiple-range tests (Table 1). When 1987 was excluded, there were no differences between years ($F_{[6,228]} = 1.358$, $P = 0.23$). Average tLPG of adult females did not correlate with March–June precipitation the previous year ($r = -0.01$) or December–March temperature ($r = 0.01$). Number of adult females and tLPG did not correlate ($r = -0.33$, $N = 8$, $P > 0.4$). Individual female bighorns did not always follow the population trend in tLPG, and every year there was considerable variation in fecal larval counts between individuals (Fig. 2).

The average tLPG of females was unrelated to the occurrence of pneumonia in 1985–1986 (Fig. 2), nor was it correlated with lamb survival to weaning ($r = -0.36$, $N = 8$, $P > 0.3$) or to 1 year of age ($r = -0.41$, $N = 8$, $P > 0.3$). When the year of the

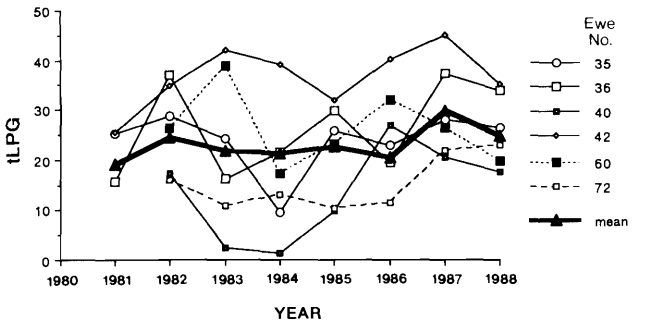

FIG. 2. Average square-root transformed counts of *Protostrongylus* spp. first-stage larvae (tLPG) collected in southwestern Alberta from adult female bighorn sheep in March–April 1981–1988 (population mean and individual values for some females monitored for 7 or 8 years).

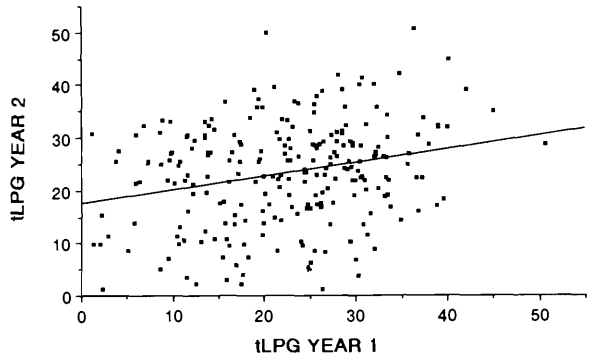

FIG. 3. Square-root transformed count of *Protostrongylus* spp. first-stage larvae (tLPG) in fecal samples collected from the same adult female bighorn sheep in successive years. Samples collected in southwestern Alberta in March–April 1981–1988.

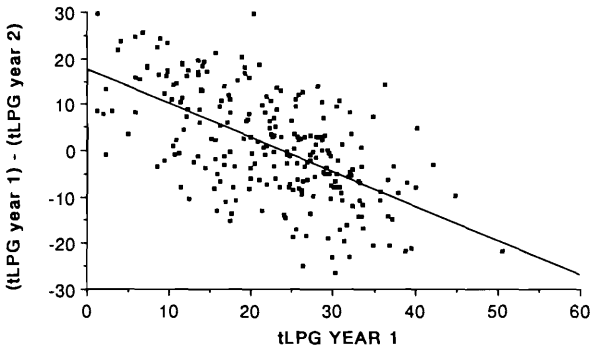

FIG. 4. Correlation between square-root transformed count of *Protostrongylus* spp. first-stage larvae (tLPG) in fecal samples of adult female bighorn sheep in one year, and change in tLPG for the same female the next year. Samples were collected in southwestern Alberta in March–April 1981–1988.

TABLE 2. Multiple regression analysis of square-root transformed numbers of *Protostrongylus* spp. first-stage larvae (tLPG) in the feces of female bighorn sheep 21 months of age and older, in March–April 1981–1986 in southwestern Alberta

Variable	*b*	SE of *b*	β	*t*	*P*
tLPG year 1	0.32	0.12	0.256	2.75	0.007
Lamb sex year 1	−5.55	2.03	−0.255	2.73	0.007
Pregnancy year 2	9.36	4.68	0.188	2.00	0.048
Constant (*a*)	19.71	6.75			

NOTE: The dependent variable is tLPG in year 2. *b*, slope.

epizootic was excluded, the correlation of mean female tLPG and lamb survival to 1 year improved ($r = -0.6$, $N = 7$, one-tailed $P = 0.078$). If both 1985 and 1986 (when lamb survival was likely affected by the epizootic) were excluded, the correlation was strong ($r = -0.91$, $N = 6$, $P = 0.006$).

If an individual's infection remained similar from year to year, and environmental and reproductive effects did not alter larval counts, one would expect a strong correlation between the numbers of larvae in fecal samples collected from the same sheep in successive years. Instead, counts from the same female in successive years were weakly correlated (Fig. 3) ($r = 0.25$, $N = 238$ female-years, $P < 0.001$). There was a negative correlation between tLPG in one year and change in tLPG the next year ($r = -0.61$, $N = 238$ female-years, $P < 0.001$). Females with a high tLPG in one year were likely to shed fewer larvae the following year, whereas those with a low tLPG were likely to show an increased count the following year (Fig. 4). The regression predicted no change at 23.81 tLPG, close to the overall mean tLPG of adult females ($N = 324$ female-years, $\bar{x} = 22.86 \pm 0.51$).

If reinfection from eating infected gastropods occurred in the winter range, the most likely time would be August–September, after some sheep have returned from the summer range and before snow and hard frosts begin. There was no correlation, however, between the number of days that a female spent in the winter range in August–September and either tLPG the following March–April ($r = 0.001$) or change in tLPG from the previous year ($r = 0.03$). In addition, days in the winter range in August–September were not correlated with tLPG the next year when the effects of lactation, lamb survival, and sex (see below) were controlled for in multiple regression models. These analyses were restricted to 1981–1986, as insufficient information on female dispersion was available for later years.

Pregnancy and lamb sex affected tLPG in 1981–1986 (Festa-Bianchet 1989*a*). These effects were confirmed when data for 1987 and 1988 were included. Pregnant females had greater tLPG values ($N = 273$ female-years, $\bar{x} = 23.39 \pm 0.55$) than those not pregnant ($N = 43$ female-years, $\bar{x} = 19.03 \pm 1.36$) ($t = 2.94$, $P = 0.003$). Most nonpregnant females were yearlings or 2-year-olds, and within these age-classes the difference in tLPG with pregnancy was significant (pregnant: $N = 54$ female-years, $\bar{x} = 24.17 \pm 1.05$; not pregnant: $N = 29$ female-years, $\bar{x} = 18.20 \pm 1.53$; $t = 3.28$, $P = 0.002$). During pregnancy there was no difference in tLPG according to fetal sex (male fetus: $N = 97$ pregnancies, $\bar{x} = 23.11 \pm 0.87$; female fetus: $N = 102$ pregnancies, $\bar{x} = 23.46 \pm 0.87$; $t = 0.28$, $P > 0.7$), but the following year females that had weaned sons had higher tLPG values than females that had weaned daughters (sons: $N = 77$ female-years, $\bar{x} = 25.41 \pm 1.18$; daughters: $N = 71$ female-years, $\bar{x} = 21.21 \pm 1.14$; $t = 2.55$, $P = 0.012$).

How much of the variance in tLPG of individual females could be explained by a combination of factors using multivariate statistics? Together, tLPG in one year, sex of lamb weaned that year, and pregnancy the following year contributed to a multiple regression, with tLPG the following year as the dependent variable in 1981–1986 (Table 2; $N = 101$ female-years, $F = 6.457$, $R^2 = 0.17$). When data collected in 1987 and 1988 were included, each independent variable remained significant, with $R^2 = 0.14$. Therefore, the proportion of

TABLE 3. Age-specific square-root transformed fecal counts of *Protostrongylus* spp. first-stage larvae of female bighorn sheep in southwestern Alberta, in March–April 1981–1988

Age (yr)	*N*	Avg.	SE
Lamb	40	27.82	1.55
1	42	22.12	1.24
2	43	22.09	1.33
3	42	22.35	1.38
4	41	24.38	1.27
5	32	23.82	1.74
6	32	22.18	1.52
7	26	22.10	1.55
8	23	23.45	2.50
>8	43	23.35	1.69

NOTE: *N*, number of females, except for those older than 8 years, where it indicates female-years.

variance explained was small. None of the independent variables in the multiple regression were correlated with each other.

Among adult females, tLPG did not vary with age, but lambs had a greater tLPG than older females (Table 3). If the data in Table 3 are analyzed with ANOVA, no differences emerge ($F_{[9,354]} = 1.42$, $P = 0.18$), but when the tLPG of lambs was compared with that of older females ($N = 324$ female-years, $\bar{x} = 22.86 \pm 0.51$) with a *t*-test, it was found to be greater ($t = 3.20$, $P = 0.001$). The difference remained if female lambs were compared with older but not pregnant females ($t = 4.28$, $P < 0.001$). Pregnant yearlings did not have a greater tLPG ($N = 21$, $\bar{x} = 25.20 \pm 1.34$) than pregnant older females ($N = 213$ female-years, $\bar{x} = 22.03 \pm 0.63$) ($t = 1.53$, $P = 0.13$). Data from 1987 were excluded, because in 1987 samples were not collected from the only pregnant yearling.

There was no consistent relationship between tLPG and reproductive success. When all years were considered, there was no relationship between female tLPG and lamb survival to either weaning or 1 year (Table 4). The relationship was significant in 1981–1984, but the trend was reversed following pneumonia in 1985.

The tLPG of females that survived to the following March–April ($N = 236$ female-years, $\bar{x} = 23.42 \pm 0.58$) was not different from that of females that died within a year ($N = 35$, $\bar{x} = 22.43 \pm 1.62$) ($t = 0.6$, $P > 0.5$). There was also no evidence that tLPG of individuals increased just before their death; when the last tLPG of females that died was compared with their average tLPG in previous years, in 11 cases females had greater tLPG in the year before their death than in previous years, but in 10 cases the pattern was reversed. On average 3.5 years of data were available for each female for this comparison.

The tLPG of female lambs was correlated with that of their mother (Fig. 5) ($r = 0.52$, $N = 26$, $P = 0.006$), but the trend for males was negative ($r = -0.34$, $N = 16$, $P > 0.1$). If data from 1987 were excluded, heart girth of female lambs was negatively correlated with tLPG ($r = -0.34$, $N = 25$, one-tailed $P = 0.05$), but there was no correlation for male lambs. Horn length and tLPG were not correlated for lambs of either sex. A female's tLPG and her daughter's heart girth the following October were negatively correlated ($r = -0.46$, $N = 20$, $P = 0.04$). The same calculation for sons, however, resulted in a nonsignificant positive trend ($r = 0.49$, $N = 11$, $P = 0.12$).

This study focussed on female reproduction, and few samples were collected from males, except for lambs and yearlings. Males had a greater tLPG than females (Table 5) (lambs: $t = 2.39$, $P = 0.02$; yearlings: $t = 2.23$, $P = 0.03$). Data from 1987 were excluded when comparing yearlings, because no samples from males were collected that year.

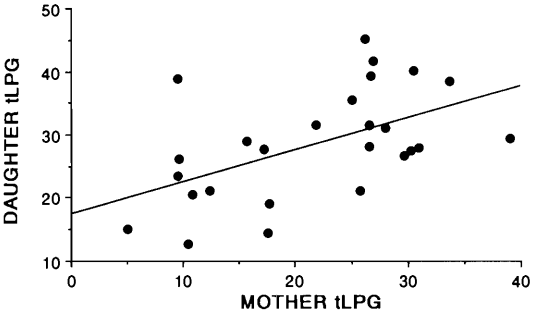

FIG. 5. Square-root transformed counts of *Protostrongylus* spp. first-stage larvae (tLPG) in fecal samples of adult female bighorn sheep and their daughters. Samples were collected in southwestern Alberta in March–April 1981–1988.

Discussion

Factors affecting larval counts

There was considerable variation in tLPG (transformed larval count) among fecal samples from the same sheep. Sources of variation include pellet weight, daily fecal production, and changes in the number of larvae produced by adult lungworms. Pellet weight varies with ash content (Seip 1983). A sheep that had recently visited a salt lick or eaten dusty forage would produce feces of high specific weight. Sheep produce more feces per day in early March than in late April (Hebert 1973). Individual counts likely retained considerable error variance, reducing the explanatory power of regressions. This problem was partly overcome by collecting several samples from each female and sampling many females each year.

Two species of *Protostrongylus* infect bighorn sheep. Of these, *P. stilesi* has been implicated in pathology of the lungs and its prevalence probably approaches 100% (Uhazy et al. 1973). *Protostrongylus rushi* has lower prevalence (38% reported by Uhazy et al. 1973) and is not known to cause significant pathology. First-stage larvae of the two species cannot be distinguished, nor is it possible to assess the intensity of infection of either species without killing the host. Therefore, the two species cannot be treated separately. The higher prevalence and intensity of *P. stilesi* relative to *P. rushi* suggest that most larval production is contributed by the former. Nevertheless, the presence of two species suggests that caution be used in interpreting the results of this study until the species-specific relationships between infection intensity, pathology, and larval production are better understood.

A more serious problem is the relationship between tLPG and intensity of infection. There are no data comparing fecal larval counts with infection intensity of individual bighorns. In domestic sheep, fecal counts of gastrointestinal nematode eggs are usually correlated with infection intensity (Boag and Thomas 1977; Douch et al. 1984). Forrester and Senger (1964) found higher larval counts in herds with more lungworm lesions in the lungs, but it is not clear how lesions and infection intensity are related. Uhazy et al. (1973) reported that counts correlated with infection intensity, but they did not include a statistical analysis. Experimental infections of bighorn lambs increase larval counts (Samson et al. 1987). It is likely, however, that

TABLE 4. Relationship between transformed fecal count of *Protostrongylus* spp. first-stage larvae of female bighorn sheep in March–April (tLPG) and their lamb's survival to weaning or to 1 year in southwestern Alberta, 1981–1988

	Lamb		Female tLPG				
	Survival to:	Survived?	*N*	Avg.	SE	*t*	*P*
1981–1988	weaning	Yes	193	23.07	0.79	0.67	0.50
		No	79	23.88	1.08		
	1 year	Yes	77	22.48	1.08	1.31	0.19
		No	150	24.11	0.70		
1981–1984	weaning	Yes	85	20.66	1.00	1.98	0.05
		No	32	24.74	2.06		
	1 year	Yes	39	18.90	1.49	2.46	0.02
		No	47	24.20	1.52		
1985–1988	weaning	Yes	108	24.97	0.77	1.19	0.24
		No	47	23.31	1.16		
	1 year	Yes	38	26.15	1.35	1.39	0.17
		No	103	24.07	0.71		

NOTE: *N*, number of female-years.

TABLE 5. Sex-specific square-root transformed fecal count of *Protostrongylus* spp. first-stage larvae of bighorn lambs and yearlings in southwestern Alberta, March–April 1981–1988

	N	Avg.	SE	*t*	*P*
Lamb					
Male	23	33.39	1.46	2.39	0.02
Female	40	27.82	1.55		
Yearling*					
Male	13	27.63	3.03	2.23	0.03
Female	40	21.53	1.22		

NOTE: *N*, number of individuals sampled.
*Data from 1987 not included (see text).

tLPG is affected by reproductive effort, stress, and hormonal changes (Festa-Bianchet 1989*a*; Gibbs and Barger 1986).

Larval counts appear dependent upon both intensity of infection and efficiency of the immune response, which in turn is dependent upon body condition. A sheep with many worms should have a greater tLPG than one with few worms, but a sheep under stress (nutritional, physiological, or reproductive) should shed more larvae than one with the same infection but not subject to stress. Survival of first-stage larvae is affected by the immune response (Butterworth 1984), and worms may increase egg production in response to a weakening of the host (Ito et al. 1986).

The tendency of individual tLPG to change towards the mean for all females (Fig. 3) may indicate competition among lungworms. At high intensities of infection, the parasites' individual reproductive success may be lower (Anderson and Michel 1977; Dobson 1986). A large number of worms may stimulate the immune system (Nettles and Prestwood 1976; Anderson and Michel 1977), perhaps leading to greater mortality for adults, eggs, or larvae.

The data do not suggest that lungworm infection is correlated with spring precipitation, as suggested by Forrester and Littell (1976), or negatively correlated with winter temperature, as proposed by Stelfox (1976). However, results from the Ram Mountain bighorn population, about 200 km northwest of Sheep River, were different. There, Jorgenson and Wishart (1986) found a significant correlation between late-spring precipitation and late-winter larval counts over 9 years ($r = 0.64$). Because of frequent chinook winds, winters at Sheep River are mild, and may not stress the sheep to the point where their immune response is adversely affected.

With the exception of 1987, the average tLPG did not vary between years, suggesting that environmental factors may not be important in its determination in most years. The sharp rise in 1987, however, was found also in a bighorn herd about 80 km northwest of Sheep River (Jorgenson 1988). No reason for this increase is apparent, but its occurrence in both herds suggests a common (but as yet unidentified) environmental cause.

The data do not support the hypothesis that early return to the winter range would increase lungworm infection (Wishart et al. 1980). Changes in intensity between years may be small, and tLPG is unsuitable for detecting them. Alternatively, the availability of infected snails is not greater in the winter than in the summer range, as assumed by Wishart et al. (1980). The role of transplacental infection (Hibler et al. 1972) in controlling fecal larval counts is unclear. If most worms were acquired transplacentally, behavior, reproductive effort, and weather may have little effect on infection intensity, even though they may affect larval production.

Sex differences

Bighorn sheep are sexually dimorphic, and body size probably has a greater effect on reproductive success in males than in females (Geist 1971). Clutton-Brock et al. (1985) found that in sexually dimorphic birds and mammals, young males are more susceptible than young females to resource shortages, and suggested that young males adopt a riskier growth strategy to achieve greater body size and, eventually, greater reproductive success. In these species, a male's reproductive success is dependent upon male–male competition, which in turn depends upon body size. Because a small-bodied male may have little or no opportunity to mate, males should take more risks than

females during growth, investing fewer resources in the fat storage necessary to survive periods of scarcity. The results of this study may be interpreted as suggesting that, compared with females, males devote more resources to growth, and invest fewer resources in the immune system, becoming more susceptible to parasites and pathogens. Not only did young males have a greater tLPG than young females, but yearling males also suffered greater mortality than yearling females in the pneumonia epizootic (Festa-Bianchet 1988*c*). The hypothesis of a trade-off between body growth and investment in the immune system may also explain why female lambs, which were still growing, had a greater tLPG than older females. Lambs of both sexes suffered higher mortality than other age-classes in the pneumonia epizootic (Festa-Bianchet 1988*c*).

The correlation in tLPG between female lambs and their mothers has at least three nonexclusive explanations. It could be due to the similarity in environment, to genetic similarities in immunocompetence, or to a correlation between a female's condition, her ability to invest in her daughter, and their resulting tLPG. A female in poor condition may have a high tLPG and be unable to provide adequate maternal investment in her daughter, which in turn would have a high tLPG. The lack of a similar correlation for male lambs suggests that investment in sons may be less dependent upon maternal condition than investment in daughters. The association between tLPG and nursing behavior is similarly stronger for female than for male lambs (Festa-Bianchet 1988*a*). The alternative that sons are less likely than daughters to share the mother's environment does not explain the lack of correlation in tLPG between mothers and sons, because lambs of both sexes remain with their mother until November. By then, the chance of ingesting infected snails is low because the ground is frozen.

It is intriguing that, in addition, the correlations between tLPG and body size and between maternal tLPG and body size were significant for female but not for male lambs. Sex-specific differences have been reported for other species of hosts and parasites. Folstad et al. (1989) found more larvae of the warble fly *Hypoderma tarandi* on male than on female reindeer (*Rangifer tarandus tarandus*), and reported that body weight was negatively correlated with infection intensity for females but not for males. Halvorsen (1986) found that male reindeer calves (but not female calves) infected with the nematode *Elaphostrongylus rangiferi* were heavier than uninfected calves.

Mothers with a high tLPG may limit their investment in daughters, possibly because they devote more metabolic resources to their immune system. This may explain the negative correlation between maternal tLPG in late winter and daughter's body size at weaning. Mothers of sons may invest at the highest possible level, regardless of tLPG. This suggestion is supported by the increase in tLPG following the weaning of sons. We may also expect greater mortality among females following the weaning of sons than of daughters, but that is not found (Festa-Bianchet 1989*a*). Overall, the data provide interesting and consistent hints that a male's strategy may involve taking risks with parasites to maximize body size. Clearly, more data are needed to further explore this possibility.

Larval counts and survival

Larval counts from individual females correlated with lamb survival before the pneumonia epizootic but not after (Table 4). There was a good correlation between average tLPG and proportion of lambs surviving to 1 year when the 2 years of the epizootic were not included, but the correlation disappeared if they were included. It could be argued that high lamb mortality in 1985 and 1986 was due to the epizootic, and therefore that those years should be excluded from this analysis.

Average tLPG may be a predictor of lamb survival in years when they are free from the effects of pneumonia; these include effects during epizootics, when sheep of all ages die of pneumonia (Onderka and Wishart 1984), and lamb mortality during the year after die-offs (e.g., 1986), which is also thought to be caused by pneumonia (Spraker and Hibler 1982). It appears that pneumonia overrides any relationship between tLPG and lamb survival, just as it overrides population processes that may otherwise be density-dependent (Wehausen et al. 1987). Lamb survival was lower after the epizootic than before it, despite lower population density (Festa-Bianchet 1989*b*).

If one accepts that tLPG and lamb survival are correlated, it still remains to be established whether the relationship is causal. I suggest that it is not, but that it reflects female condition. Females in poor condition may be unable to limit reproduction of parasites, and be susceptible to reinfection. These females may also be unable to provide sufficient investment in their offspring to ensure their survival. Lungworm infection may further debilitate females already in poor condition, but the relative role of lungworms in lowering reproductive performance remains unclear.

Are larval counts useful for monitoring herd health?

Collecting and analyzing several hundred fecal samples from marked bighorn sheep is a time-consuming procedure which can only be used for herds that are easily accessible and habituated to human observers. This study suggests that tLPG may be useful for predicting lamb survival to 1 year, but not for predicting female survival or pneumonia epizootics. The link between tLPG and lamb survival is, at best, limited to years without pneumonia.

Despite the opportunity to monitor a marked bighorn population during an outbreak of pneumonia, this study could find no evidence suggesting a link between infection with *Protostrongylus* spp. and pneumonia. Recent evidence suggests that pneumonia is a bacterial disease independent of lungworm infection (Foreyt and Jessup 1982; Samson et al. 1987; Onderka and Wishart 1988), and the emphasis on lungworms as a cause of pneumonia may be unwarranted.

For bighorn sheep, the "normal" state appears to be one of infection with lungworms. The suggestion that lungworm larval counts can predict pneumonia epizootics (Stelfox 1971; Uhazy et al. 1973) is not supported by long-term data. Comparisons of tLPG among herds may similarly prove to be of little use. For example, bighorns at Ram Mountain have consistently shown higher larval counts than those at Sheep River, yet no pneumonia epizootic is known to have ever occurred in the Ram Mountain herd, which has been monitored since 1971 (J. T. Jorgenson, personal communication).

The usefulness of larval counts would decrease if samples were not collected from known individuals (or at least those of known sex–age class), or if untransformed LPG values were used to derive population means. A few individuals with high counts could give a false impression of high average counts, particularly if these individuals were sampled repeatedly in one collection (e.g., if samples were collected from bedding sites).

The sharp rise in tLPG in 1987 may have been a cause for concern. Yet no pneumonia followed, the population was

slowly increasing, and the next year the average tLPG was back to the level of 1981–1986.

In conclusion, I suggest that fecal larval counts are not a reliable gauge of herd health. Demarais et al. (1983) reached a similar conclusion after monitoring white-tailed deer (*Odocoileus virginianus*) abomasal parasites over 4 years. Further research should explore the relationships between tLPG and infection intensity, and between infection intensity and reproductive performance. This would best be done with captive bighorns, where infection, reinfection, nutrition, reproduction, and environment can be monitored and manipulated.

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ANDERSON, R. M., and MICHEL, J. F. 1977. Density-dependent survival in populations of *Ostertagia ostertagi*. Int. J. Parasitol. **7**: 321–329.

BOAG, B., and THOMAS, J. 1977. Epidemiological studies on gastrointestinal nematode parasites of sheep: the seasonal number of generations and succession of species. Res. Vet. Sci. **22**: 62–67.

BUTTERWORTH, A. E. 1984. Cell-mediated damage to helminths. Adv. Parasitol. **23**: 143–235.

CLUTTON-BROCK, T. H., ALBON, S. D., and GUINNESS, F. E. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature (London), **313**: 131–133.

DEMARAIS, S., JACOBSON, H. A., and GUYNN, D. C. 1983. Abomasal parasites as a health index for white-tailed deer in Mississippi. J. Wildl. Manage. **47**: 247–252.

DOBSON, A. P. 1986. Inequalities in the individual reproductive success of parasites. Parasitology, **92**: 675–682.

DOUCH, P. G. C., HARRISON, G. B. L., BUCHANAN, L. L., and BRUNSDON, R. V. 1984. Relationship of histamine in tissues and antiparasitic substances in gastrointestinal mucus to the development of resistance to trichostrongyle infections in young sheep. Vet. Parasitol. **16**: 273–288.

FESTA-BIANCHET, M. 1986. Seasonal dispersion of overlapping mountain sheep ewe groups. J. Wildl. Manage. **50**: 325–330.

——— 1988*a*. Nursing behaviour of bighorn sheep: correlates of ewe age, parasitism, lamb age, birthdate, and sex. Anim. Behav. **36**: 1445–1454.

——— 1988*b*. Age-specific reproduction of bighorn ewes in Alberta, Canada. J. Mammal. **69**: 157–160.

——— 1988*c*. A pneumonia epizootic in bighorn sheep, with comments on preventive management. *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Banff, Alta., April 1988. Vol. 6. *Edited by* W. M. Samuel. Alberta Fish and Wildlife, Edmonton. pp. 66–76.

——— 1989*a*. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). J. Anim. Ecol. **58**: 785–795.

——— 1989*b*. Survival of male bighorn sheep in southwestern Alberta. J. Wildl. Manage. **53**: 259–263.

FESTA-BIANCHET, M., and JORGENSON, J. T. 1985. Use of xylazine and Ketamine to immobilize bighorn sheep in Alberta. J. Wildl. Manage. **49**: 162–165.

FOLSTAD, I., NILSSEN, A. C., HALVORSEN, O., and ANDERSEN, J. 1989. Why do male reindeer (*Rangifer t. tarandus*) have higher abundance of second and third instar larvae of *Hypoderma tarandi* than females? Oikos, **55**: 87–92.

FOREYT, W. J., and JESSUP, D. A. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. J. Wildl. Dis. **18**: 163–168.

FORRESTER, D. J., and LITTELL, R. C. 1976. Influence of rainfall on lungworm infection in bighorn sheep. J. Wildl. Dis. **12**: 48–51.

FORRESTER, D. J., and SENGER, C. M. 1964. A survey of lungworm infections in bighorn sheep in Montana. J. Wildl. Manage. **28**: 481–491.

GEIST, V. 1971. Mountain sheep. University of Chicago Press, Chicago.

GIBBS, H. C., and BARGER, I. A. 1986. *Haemonchus contortus* and other trichostrongylid infections in parturient, lactating and dry ewes. Vet. Parasitol. **22**: 57–66.

HALVORSEN, O. 1986. On the relationship between social status of host and risk of parasitic infection. Oikos, **47**: 71–74.

HEBERT, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. thesis, University of British Columbia, Vancouver.

HIBLER, C. P., LANGE, R. E., and METZGER, C. J. 1972. Transplacental transmission of *Protostrongylus* spp. in bighorn sheep. J. Wildl. Dis. **8**: 39.

ITO, A., KANO, S., HIOKI, A., KASUYA, S., and OHTOMO, H. 1986. Reduced fecundity of *Hymenolepis nana* due to thymus-dependent immunological responses in mice. Int. J. Parasitol. **16**: 81–85.

JORGENSON, J. T. 1988. Environmental impact of the 1988 Calgary Winter Olympics on Mt. Allan bighorn sheep. *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Banff, Alberta, April 1988. Vol. 6. *Edited by* W. M. Samuel. Alberta Fish and Wildlife, Edmonton. pp. 121–134.

JORGENSON, J. T., and WISHART, W. D 1986. Ram Mountain bighorn sheep project. Progress report 1984 and 1985. Alberta Energy and Natural Resources, Fish and Wildlife Division, Edmonton.

KERLINGER, F. N., and PEDHAZUR, E. J. 1973. Multiple regression in behavioral research. Holt, Rinehart and Winston, New York.

MACHLIS, L., DODD, P. W. D., and FENTRESS, J. C. 1985. The pooling fallacy: problems arising when individuals contribute more than one observation to the data set. Z. Tierpsychol. **68**: 201–214.

MARSH, H. 1938. Pneumonia in Rocky Mountain bighorn sheep. J. Mammal. **19**: 214–219.

NETTLES, V. F., and PRESTWOOD, A. K. 1976. Experimental *Parelaphostrongylus andersoni* infections in white-tailed deer. Vet. Pathol. **13**: 381–393.

ONDERKA, D. K., and WISHART, W. D. 1984. A bighorn die-off from pneumonia in southern Alberta (1982–83). *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Whitehorse, Y.T., 30 April – 3 May 1984. Vol. 4. *Edited by* M. Hoefs. Yukon Wildlife Branch, Whitehorse. pp. 356–363.

——— 1988. Experimental contact transmission of *Pasteurella hemolytica* from clinically normal domestic sheep causing pneumonia in Rocky Mountain bighorn sheep. J. Wildl. Dis. **24**: 663–667.

SAMSON, J., HOLMES, J. C., JORGENSON, J. T., and WISHART, W. D. 1987. Experimental infection of free-ranging Rocky Mountain bighorn sheep with lungworms (*Protostrongylus* spp.; Nematoda: Protostrongylidae). J. Wildl. Dis. **23**: 396–403.

SAMUEL, W. M., and GRAY, J. B. 1982. Evaluation of the Baermann technique for recovery of lungworm larvae from wild ruminants. *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Forst Collins, CO, 17–19 March 1982. Vol. 3. *Edited by* G. G. Schoonveld. Colorado Division of Wildlife, Denver. pp. 25–33.

SEIP, D. R. 1983. Foraging ecology and nutrition of Stone's sheep. Ph.D. thesis, University of British Columbia, Vancouver.

SOKAL, R. R., and ROHLF, F. J. 1981. Biometry. W. H. Freeman and Co., San Francisco.

SPRAKER, T. R. 1979. The pathogenesis of pulmonary protostrongy-

losis in bighorn lambs. Ph.D. thesis, Colorado State University, Boulder.

SPRAKER, T. R., and HIBLER, C. P. 1982. An overview of the clinical signs, gross and histologic lesions of the pneumonia complex of bighorn sheep. *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Fort Collins, CO, 17–19 March 1982. Vol. 3. *Edited by* G. G. Schoonveld. Colorado division of Wildlife, Denver. pp. 163–172.

SPSS INC. 1983. SPSS user's guide. McGraw-Hill, New York.

STELFOX, J. G. 1971. Bighorn sheep in the Canadian Rockies. A history 1800–1970. Can. Field-Nat. **85**: 101–122.

——— 1976. Range ecology of Rocky Mountain bighorn sheep. Can. Wildl. Serv. Rep. Ser. No. 39.

UHAZY, L. S., HOLMES, J. C., and STELFOX, J. G. 1973. Lungworms in the Rocky Mountain bighorn sheep of western Canada. Can. J. Zool. **51**: 817–824.

WEHAUSEN, J. D., BLEICH, V. C., BLONG, B., and RUSSI, T. L. 1987. Recruitment dynamics in a southern California mountain sheep population. J. Wildl. Manage. **51**: 86–98.

WISHART, W. D., JORGENSON, J. T., and HILTON, M. 1980. A minor die-off of bighorns from pneumonia in southwestern Alberta. *In* Proceedings of the Biennial Symposium of the Northern Wild Sheep and Goat Council, Salmon, ID, April 23–25, 1980. Vol. 2. *Edited by* W. O. Hickey. Idaho Fish and Game Department, Salmon. pp. 229–245.