Seasonal Fluctuation and Inhibited Development of Populations of Dictyocaulus filaria in Ewes and Lambs

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ABSTRACT

The fluctuation of populations of Dictyocaulus filaria in sheep was studied under field conditions in which animals are housed during the winter and grazed from late spring to autumn. A comparison was made between residual pasture contamination with overwintered larvae, the fecal larval deposition by ewes from June and both of these factors combined as sources of infection for spring born lambs. Ewes and lambs were killed serially over a year and worms were recovered from the lungs and counted. It was found that during the stabling period most of the ewes were carrying moderate numbers of D. filaria. However, while the vast majority of lungworm populations in the winter was inhibited in development at the early fifth larval stage, virtually all worms in the spring were adults. Any one source of infection studied contributed to the acquisition of important burdens of D. filaria by lambs as well as ewes. Worm counts reached peak in all lambs by November and this pointed to only one important Dictyocaulus generation per grazing season. It would also appear that larvae picked up by ewes and lambs as the grazing season advanced had become inhibited in development with the inhibition rate being most marked in autumn.

RÉSUMÉ

Cette étude visait à déterminer les fluctuations du nombre de Dictyocaulus filaria chez des moutons hivernés dans une bergerie et envoyés au pâturage, de la fin du printemps jusqu'à l'automne. On compara l'influence de la contamination résiduelle des pâturages attribuable aux larves ayant survécu à l'hiver avec celle qui résulte des larves éliminées dans les fèces des brebis, à compter du mois de juin, comme source d'infestation pour les agneaux. On abattit des brebis et des agneaux à différentes périodes de l'année et on compta les nématodes qu'on récupéra de leurs poumons. On réalisa qu'au cours de l'hiver la plupart des brebis étaient porteuses d'un nombre peu élevé de D. filaria. En dépit du fait que, durant l'hiver, la plupart de ces parasites subissaient une inhibition de leur développement, au début du cinquième stade larvaire, ils avaient presque tous atteint la maturité au printemps. N'importe laquelle des sources d'infestation qu'on explora s'avéra susceptible de provoquer une dictyocaulose marquée, tant chez les agneaux que chez les brebis. C'est en novembre que le comptage de D. filaria atteignit un point culminant, chez tous les agneaux; ceci permit de conclure à une seule génération importante du parasite, au cours d'une saison de paissance. Il semblerait également que les larves ingérées par les brebis et les agneaux, au

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fur et à mesure que progressait la période de paissance, subirent l'inhibition, surtout au cours de l'automne.

INTRODUCTION

It is well documented that strongyle populations in spring born lambs emerge from two sources, namely, the fecal egg deposition by ewes and the overwinter survival of larvae on pasture (3, 8, 23, 27). However, the literature on the relative significance of the ewe fecal larval output and of the residual pasture contamination as sources of infection with *Dictyocaulus filaria* is limited.

Dictyocaulus appears to be common in sheep in various parts of Canada (9, 18, 22, 26) and the infections could reach epidemic proportions in some parts of the country (5, 18). In the Rimouski region (Eastern Quebec), where the present investigation has been carried out, over 80% of the sheep population could be infected at certain times of the year (5). Therefore, it was decided to study the sources and the trend of *D. filaria* burdens in sheep under the field conditions in which animals are grazed from June to October-November and are then stabled in unheated pens for the winter months and most of the spring (November-May).

MATERIALS AND METHODS

Experimental design

Early in the fall (September) of 1970, 105 adult ewes and five rams of Leicester-Cheviot-Dorset crosses of mixed ages were chosen at random from several flocks of the region and were moved to a local property. These animals had all run during the entire grazing season of 1970 on permanent pastures which were presumably contaminated with lungworms and gastrointestinal parasites of sheep. Furthermore, fecal examination by the flotation technique in October confirmed that most of these sheep were infected with *D. filaria*. The ewes were bred in October and were subsequently housed in pens where reinfection was considered minimal. Following lambing each ewe was run with a single lamb.

Excepting a number of ewes and lambs which were kept indoors until July, three groups of lambs, ranging in age from three to four months, were chosen at random and were allowed to graze from June 19, 1971 on different plots according to the following plan:

Group 1: Ten lambs and ten ewes were grazed on a two acre field (Plot 1) which was double fenced. This plot was considered to be "clean" as it had not been grazed by sheep during the previous several seasons when it was ploughed and reseeded.

Group 2: Eighteen lambs were allowed to graze alone on a two acre field (Plot 2) which was double fenced. This plot was part of a permanent pasture and since it had been grazed in the previous season by sheep known to be infected with *D. filaria* it was assumed to be "contaminated" with overwintered larvae.

Group 3: Twelve lambs were turned out with 18 ewes on a three acre, double fenced field (Plot 3). This plot was also part of the permanent pasture from which Plot 2 was fenced off. Therefore, Plot 3 was considered to be equally "contaminated" as Plot 2.

Fecal examination at the time of pasturing had revealed that several of each of Groups 1 and 2 ewes and a number of the ewes remaining in stable were infected with *D. filaria*. However, similar examination of all lambs in June coupled with examination of the lungs at necropsy of two stabled lambs in July showed that no lamb was infected during the stabling period and this confirmed that acquisition of infection in pens was practically nil. The principal purpose for the three grazing regimes was, therefore, to determine the relative significance of fecal larval deposition by ewes (Group and Plot 1), of over-wintering larvae on pasture (Group and Plot 2) or of both of these combined (Group and Plot 3) as sources for lamb infection.

Dictyocaulus counts at necropsy of ewes and lambs

During the stabling period, groups of ewes were chosen at random and killed in

December 1970, April, May, June and July 1971. Groups of lambs and, wherever applicable, their dams were chosen at random from each plot and killed in July, August and November, but these animals were kept in pens for at least 18-21 days before slaughter. The lungs and trachea were removed intact and the respiratory passages washed twice with one litre of warm physiological saline. Subsequently, the bronchial tree was laid open with a pair of scissors and visible worms were removed with forceps and added into the lung washing. Washings were stored in 5% formaline until examined. Portions of the washings were placed in dishes with 2 mm grid and all *D. filaria* were counted under the stereoscopic microscope. The total body length of a few of the large worms in each specimen was measured individually. Also, the first 100 small worms were measured, but wherever less than 100 of these worms were recovered all were measured. Worms were classed into immatures (inhibited in development) if <3 mm in length, and adults (developing and sexually mature forms). This classification was aided by Michel (12, 13) Michel and McKenzie (16) and Wilson (31).

RESULTS

Ewes stabled from November to July

The total number of worms and the percentage of immature forms in individual ewes at necropsy is shown in Table I. During the winter and spring the majority of ewes was infected with a moderate number of *D. filaria*. In June only two out of nine ewes were infected and by July no worm was recovered in any of the seven ewes killed at that time. Measurements of worm length are not included in the results but populations recovered from individual animals had varied in length from <2 to 3 mm for immatures at the early fifth larval stage and from 10 mm to over 6 cm for developing forms and adults. It can be seen that in December (winter) the vast majority of *Dictyocaulus* populations was inhibited in development, whereas virtually all the worms recovered from April were sexually mature.

Grazing ewes and lambs

The data of the worm counts in grazing ewes and lambs are shown in Table II. No ewe was killed in July but in two lambs (one from Plot 1 and another from Plot 3) killed at that time lungworms were not present. By August, only a small number of worms was recovered in few of the lambs of each group, although several of the ewes on Plots 1 and 3 were infected with substantial numbers of lungworms. In November, however, most of the lambs were carrying a dramatically increased number of *Dictyocaulus*. In contrast, the worm count in ewes did not change greatly between August and November. On the average, some 52% of the worm population in ewes killed in August were inhibited in development. At that time, only adult worms were recovered in the few lambs that were infected, although in one lamb 75% of the worm burden were immature. In the fall, however, over 88% and 64% of *Dictyocaulus* populations in ewes and lambs, respectively, were inhibited in development.

It can be surmised that the course of the build up of *Dictyocaulus* populations in grazing ewes was essentially similar between groups at any one time of necropsy. Therefore, in order to depict the seasonal trend of fluctuation of worm populations in ewes over the year, the group mean worm counts are pooled and summarized graphically as in Fig. 1. The individual group mean worm counts of the lambs are also shown in this figure. Similarly, since the incidence of larval inhibition had increased in both ewes and lambs as the grazing season advanced, the overall mean percentage of immatures for each date of necropsy is derived from pooled data of ewes and lambs killed at that time. Using these means, along with those for ewes killed during the stabling period, the adult/immature changes in sheep over the year are best described in Fig. 2. It is thus clear that both the fluctuation in worm counts (Fig. 1) and the change in the adult/immature proportions (Fig. 2) were markedly seasonal.

The monthly mean maximum and minimum temperature and the mean monthly total precipitation in the Rimouski area during the present experiment are presented in Table III. These data were taken from the Monthly Records of the Meteorological Observations, Canadian Department of Atmospheric Environment Service.

TABLE I. The Total Number of *D. filaria* and the Percentage of Inhibited Larvae at Necropsy of Ewes During the Stabling Period (November 1970 — July 1971)

Date of Necropsy	Ewe No.	*D. filaria* Total	*D. filaria* % Larvae
	10	0	—
	29	12	100
	31	46	100
30/12/70	63	15	90
	74	20	100
	75	17	33
	93	0	—
	109	0	—
	13	52	0
	43	28	0
	44	0	—
	46	0	—
15/04/71	61	110	0
	68	206	10
	69	50	20
	72	0	—
	78	18	0
	16	41	0
15/05/71	71	0	—
	90	75	0
	19	92	0
	24	0	—
	35	98	0
	60	0	—
17/06/71	65	0	—
	66	0	—
	99	0	—
	101	0	—
	102	0	—
	20	0	—
	42	0	—
	73	0	—
20/07/71	77	0	—
	85	0	—
	100	0	—
	106	0	—

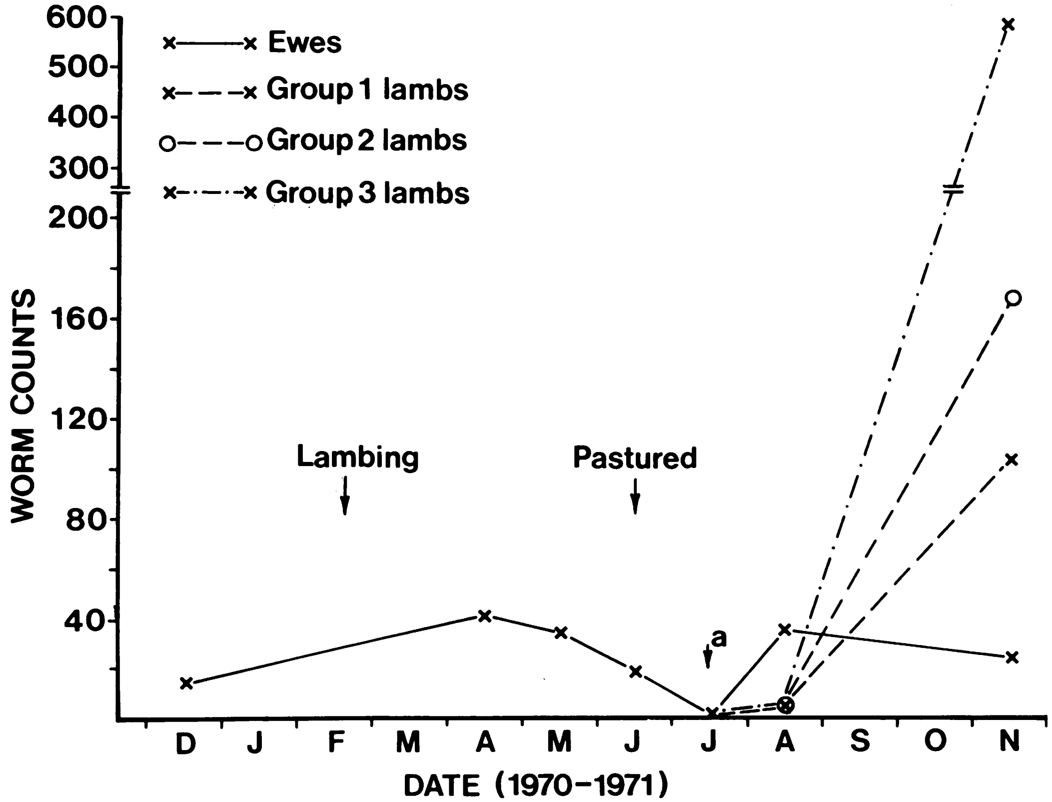

Fig. 1. The mean of total counts of D. filaria in ewes andlambs necropsied at different months. The data of Groups 1 and 3 ewes were pooled. [a] July counts as assessed from data of stabled ewes and grazing lambs necropsied at that time.

DISCUSSION

Other workers have shown that following field infections with *D. filaria* most lambs develop an effective resistance which prevents reinfections in subsequent years (21) and that this type of resistance may last for up to 46 months in naturally immunized ewes (31). That most of the present ewes had picked up a substantial number of lungworms in August is therefore somewhat surprising. These animals would be expected to have been sufficiently immunized by reason of past infections, at least that from the previous season. It may be noted, however, that Wilson (31) has also presented evidence that strength of immunity to *D. filaria* is dependent upon the level and number of infecting doses as well as upon the length of time between the last infection and the challenging dose. Having seen ewes being reinfected, Rose (21) attributes this to a breakdown of resistance. Furthemore, Michel and Coats (15) report that early in the grazing season immune cattle succumb to new infections with *D. viviparus* as do nonimmune animals, thus reconciling with the claim that acquired resistance to this lungworm may wane in from three to six months (16). A combination of factors might have therefore precipitated circumstances favorable for reinfection of the present ewes. These circumstances may well emerge seasonally and it is apparent that over 65% of the ewe population in this area may be lungworm carriers every winter. In fact, the results here show that the majority of ewes were infected with a substantial number of *D. filaria* which did not appear to fluctuate greatly through most of the year, although worm counts were lowest from late spring to early summer.

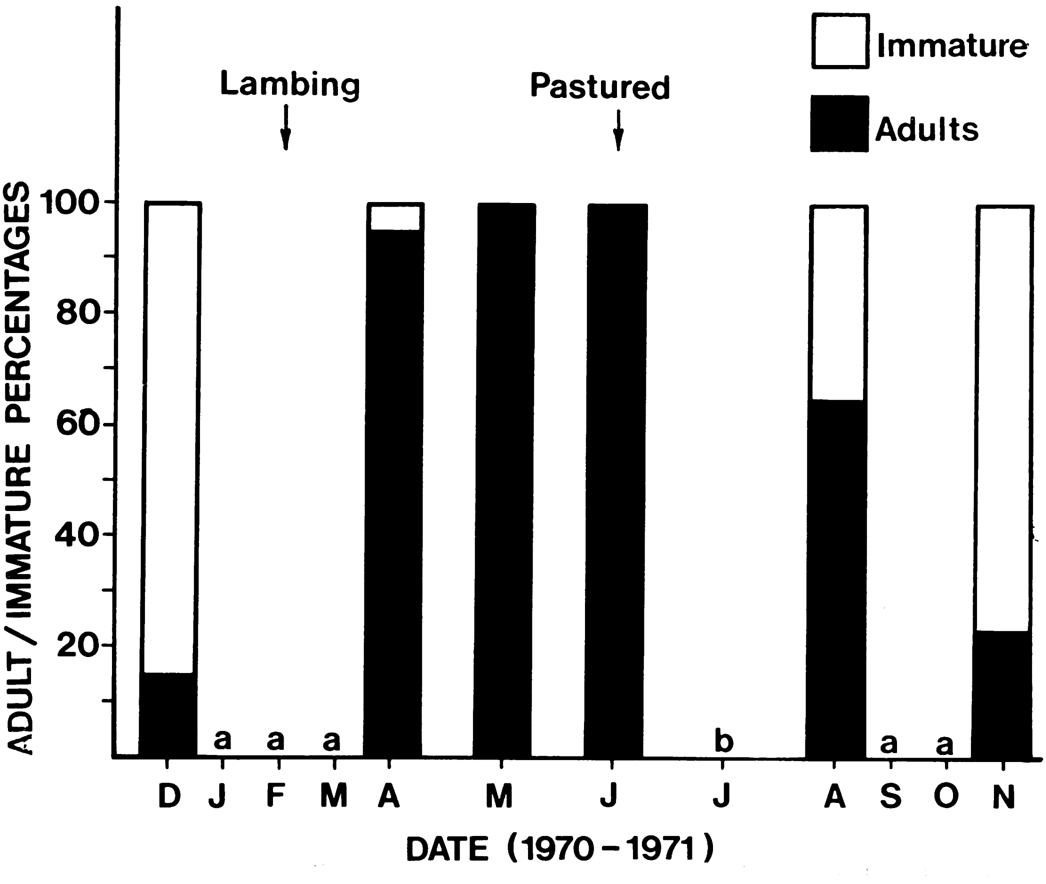

Fig. 2. The overall mean percentages of the adult/immature D. filaria in sheep. The data of grazing ewes and lambs were pooled. [a]No animals were killed. [b]No worms recovered in seven stabled ewes and two grazing lambs.

Whereas 50% of the number of sheep necropsied over the year in the present work were infected with *D. filaria,* in 70% of these animals large numbers of lungworms inhibited in development were seen. Inhibited development of *D. filaria* in sheep has been previously described by several workers, including Taylor and Michel (28), Michel (12), Thomas *et al* (30) and Wilson (31), but what seems to characterize the present lungworm populations is the seasonal trend in the change of the adult/immature proportions. Thus, during the stabling period, of *D. filaria* populations recovvered from ewes necropsied in the winter over 88% were inhibited in development, but this proportion was reversed in favor of adult worms in the spring. It would also seem that the vast majority of infective larvae picked up by ewes or lambs as the grazing season advanced had become inhibited so that by November in excess of 70% of the lungworm population in all animals were immature. The cause for the massive inhibition of *D. filaria* is not determined. However, inhibition of this lungworm has been attributed to acquired immunity (12, 30, 31). Indeed, it is a widely held concept that inhibition of strongyle development also in other host-parasite systems, including gastrointestinal nematodes in sheep, is a sequel of acquired resistance (24). Nonetheless, in recent years evidence has been produced showing that inhibition of these nematodes may be triggered also by factors other than acquired immunity, the principal factors being related broadly to either parasite induced effects (1, 6, 25) or to host induced effects (1, 2). One or more of the proposals may perhaps explain, to some degree, some of the present results. For example, that a substantial number of *Dictyocaulus* were less refractory to larval inhibition in ewes in August might suggest that these animals were somehow resistant. However, since

TABLE II. The Total Number of *D. filaria* and the Percentage of Inhibited Larvae at Necropsy of Ewes and Lambs (Groups 1, 2 and 3) Grazing From June 19-November 1971

Date of Necropsy	Group and Plot	Lamb No.	*D. filaria* Total	*D. filaria* % Larvae	Ewe No.	*D. filaria* Total	*D. filaria* % Larvae
25/07/71	1	252	0	—	—	—	—
	3	255	0	—	—	—	—
24/08/71	1	244	0	—	5	65	48
		247	0	—	30	50	40
		253	13	0	40	21	62
		—	—	—	55	0	—
	2	239	0	—	—	—	—
		259	19	0	—	—	—
		264	0	—	—	—	—
		265	0	—	—	—	—
	3	228	0	—	—	—	—
		230	8	0	58	0	—
		234	12	75	67	47	45
		240	0	—	76	63	67
		243	0	—	—	—	—
15/11/71	1	227	220	68	8	10	100
		235	14	0	25	35	75
		237	145	80	38	0	—
		250	33	100	—	—	—
	2	236	204	80	—	—	—
		249	108	0	—	—	—
		257	283	64	—	—	—
		262	0	—	—	—	—
		270	250	96	—	—	—
	3	246	0	—	1	0	—
		251	1222	74	28	58	80
		256	569	83	36	39	100

TABLE III. Monthly Temperature and Precipitation from October 1970 to November 1971, in the Rimouski Region

Year	Month	Temperature (°F) Mean maximum	Mean minimum	Mean daily	Total Precipitation (inches)	Snowfall (inches)
1970............	October	53.1	37.6	45.4	4.01	6.0
	November	41.1	28.6	34.9	2.54	11.0
	December	18.5	5.7	12.1	2.90	29.0
1971............	January	15.8	1.2	8.5	2.40	20.0
	February	21.3	5.2	13.3	2.10	21.0
	March	32.1	18.6	25.4	4.43	40.0
	April	41.6	29.0	35.3	3.50	15.0
	May	57.8	40.0	48.9	2.28	0
	June	68.3	49.0	58.7	0	0
	July	73.4	54.4	63.9	2.03	0
	August	69.7	51.8	60.8	6.77	0
	September	63.3	46.6	55.0	1.23	0
	October	52.4	39.1	45.8	3.28	0
	November	34.7	24.0	29.4	4.02	30

there was little or no infection in most of the lambs in August, it is hard to conceive that a strong immunity could have been responsible for the massive inhibition of lungworms seen in these animals in November. Alternatively, the possibility that larval inhibition might have been induced also by effects of the autumn environmental conditions on host or parasite cannot be entirely eliminated.

As to the fate of inhibited *D. filaria* larvae, the literature is not extensive. Taylor and Michel (29) indicate that dormant *Dictyocaulus* could persist in sheep for up to 100 days. Wilson (31), however, has shown that virtually all larvae may be eliminated within a short time following inhibition in immune sheep, but he also presents evidence that host resistance may vary with the size and number of immunizing exposures. In any event, the data presented here show that a substantial number of lungworms that were inhibited during autumn and winter were able to resume development massively resulting in sexually mature worms in the following spring. This finding seems to be comparable to that believed to be the case with the so-called lungworm *(D. viviparus)* "carrier" cattle (10, 11, 15, 17) and indeed it is analogous to the phenomenon of spring-rise in sheep (3, 4. 7). The triggering mechanism for the resumption of development of the inhibited *D. filaria* has not been determined but it may be viewed in the light of the various hypotheses put forward to explain spring-rise with the major proposals including the waning of acquired immunity (24) and hormonal changes associated with lactation (7) or time of year (7).

Perhaps of considerable importance epidemiologically is the maturation of the inhibited larvae in ewes at a time when susceptible lambs are turned out on pasture. Thus, apparently the fecal larval deposition by ewes on the "clean" plot from June had resulted in a significant burden of lungworms in lambs (Group 1) by November as well as in reinfections of the ewes. These results lend support to the view that *Dictyocaulus* "carrier" sheep through winter may provide a source of infection for lambs during the spring in the U.K. (19, 30), although Rose (20, 21) has minimized the importance of ewes. However, it is interesting that "carrier" cattle in the British Isles (11, 17) as well as in Eastern Canada (10) have been shown to be important contributors to the acquisition of *D. viviparus* burdens by young animals.

Rose (19, 20, 21) has shown that free-living stages of *D. filaria* are able to overwinter on pastures from which major infections of lambs derive the following spring in England. This method of strongyle transmission has also been amply demonstrated with several gastrointestinal nematodes of sheep (3, 23, 27) as well as with *D. viviparus* (10) in Canada. The data of Group 2 lambs provide evidence that also *D. filaria* larvae are able to overwinter on pasture in Eastern Canada and that they do serve a major source of infections for sheep the following season. It is interesting that, in fact, the course of infections in lambs of Group 2 closely resembled that seen in lambs of Group 1. The trend of the infection in Group 3 animals in August might also be considered essentially similar to that seen in Groups 1 and 2 animals at that time. During the fall, however, the number of worms in lambs of the former group was more than four times the number seen in lambs of the latter groups. This is understandable because, consequent to the ewe larval deposition on an already contaminated plot 3 (overwintered larvae), a greater degree of larval accumulation might have occurred on that plot. While the risk from management practices such as depicted on Plots 1 and 2 cannot be taken lightly, conditions of Plot 3 may perhaps be considered as most typical of the majority of properties in the Rimouski area where ewes and lambs are commonly grazed together on permanent pastures.

The trend of the build up of *Dictyocaulus* populations in ewes and lambs during the grazing season suggests that infective larvae were not available in a substantial number on any plot before July-August. It is interesting to note that greater numbers of lungworms were acquired by ewes than by lambs in August and this cannot be satisfactorily explained, except that the discrepancy might probably be related in part to differences in grazing ability and capacity as between ewes and their newly weaned lambs. Nevertheless, in concurrence with the findings of Thomas *et al* (30) and Ayalew *et al* (5), worm burdens had increased dramatically in the majority of lambs in autumn. This might be largely consistent with the finding of Rose (19) in that accumulation of the infective larvae on pasture is maximum during the cooler and wet periods. Although most favorable weather conditions for lungworm transmission in the present area would then seem to have been met from mid-August to October, there was no increase in the worm burdens of ewes between August and November. It might be that a higher degree of ewe resistance to establishment of lungworms (12, 31) or some other regulatory mechanism (14) was operating during the latter part of the grazing season. In this connection, it may be noted that Michel (13) has furthermore produced evidence that a substantial proportion of *D. filaria* numbers is lost during the prepatent period by way of the bronchial mucus, that this phenomenon is not related to immune responses but that it is less likely to take place if the infecting dose is small, if the host is young or if it is severely affected. In any event, the great bulk of worm populations in the present lambs in November may be referable to larvae picked up most likely in September-October. There appear to be, therefore, not more than one important generation of *Dictyocaulus* in lambs per grazing season, which conforms with similar conclusions drawn by Michel (14) regarding *D. viviparus* in cattle.

Taken together, the data here suggest that lungworm burdens in sheep fluctuate seasonally and hence, for practical purposes, may be predictable as a flock phenomenon. It should be possible therefore to devise more rational systems of control of the infections.

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