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Author(s): James H. Turner

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EXPERIMENTAL STRONGYLOIDIASIS IN SHEEP AND GOATS. II. MULTIPLE INFECTIONS: DEVELOPMENT OF ACQUIRED RESISTANCE

JAMES H. TURNER

Animal Disease and Parasite Research Division, Agricultural Research Service U. S. Department of Agriculture, Beltsville, Maryland

The writer (1955, 1959) previously reported that lambs and kids were clinically affected when experimentally exposed to single, cutaneous applications of large numbers of infective larvae of *Strongyloides papillosus*. Animals exposed to 100,000 or more larvae usually died, whereas others exposed to fewer than 100,000 larvae developed nonfatal clinical infections. The purpose of this paper is to report the results of an experiment on the resistance to challenge of lambs and kids previously exposed to immunizing infections, which the writer (1956) previously reported only in abstract.

Some evidence of acquired resistance to infection with *Strongyloides* spp. in various animals has been reported by a few workers. Sandground (1928) stated that once an infection of *S. stercoralis* was established in dogs it conferred a very effective and lasting immunity. Sheldon (1937a, b) also was successful in inducing an acquired immunity in rats to *S. ratti* after serial injections of small doses of infective larvae, and also reported the acquisition and retention of an almost absolute resistance after one previous infection was allowed to run its course and disappear. Later (1937c) he reported a sudden loss of *S. ratti* from rats 30 days after infection, which he believed indicated the development of acquired resistance. Enigk (1952a) concluded that acquired immunity prevented reinfection of adult sows with *S. ransomi*. Turner and Wilson (1958) reported the spontaneous cessation of an epizootic of strongyloidiasis in a lamb flock, which may have been due, in part, to the development of acquired resistance.

EXPERIMENTAL PROCEDURES

The 11 Shropshire lambs and 3 Toggenburg goats used in this investigation were raised parasite-free and were maintained in an isolation building in the same manner as has been previously described by Turner (1959). The techniques used in culturing infective larvae, inducing experimental infections, making the clinical observations, and recovering the parasites were also the same as those described in that paper. The feces were examined for eggs of *S. papillosus* daily for the first 3 weeks of the experiment and twice a week thereafter. All experimental animals were weighed at weekly intervals.

Eight lambs, 9 weeks old, were selected for the experiment to determine the degree of resistance elicited by repeated artificial percutaneous exposures to larvae of S. papillosus. These animals were kept in pairs in clean pens in the isolation building mentioned above. Six of these lambs were exposed to infective larvae of S. papillosus as shown in Table I and 2 served as un-

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Table I.—Data on challenged and unchallenged lambs kept in pens and exposed to 10 immunizing percutaneous applications of infective larvae of S. papillosus and their respective controls.

No. Lamb	Age and Weight at Time of Initial Infection		Immu- nizing Expo- sures* No. of Larvae		Age and Weight at Time of Challenge		Chal- lenge Expo- sure No. of Larvae	Interval Between First Exposure or Challenge	S. papillosus Recovered		
									No.	% of Larvae	Aver-
	(days)	(lb.)	(per ex- posure)	(total)	(days)	(lb.)	Barvac	and Autopsy (days)	2.00.	Admin- istered	%
					Challe	enged L	ambs				
642	61	20	10,000	100,000	133	42	300,000	33	4,188	1.05	
$\begin{array}{c} 617 \\ 623 \end{array}$	60 60	24 1/2	20,000	200,000	132	$43\frac{1}{2}$	300,000	33	8,028	1.61	1.03
023	60	$22\frac{1}{2}$	30,000	300,000	132	$42\frac{1}{2}$	300,000	33	2,543	0.42	
010	0.4	00	40.000	400.000	Unchal	lenged	Lambs				
612	61	20	10,000	100,000	133	33 1/2	-	105	980	0.98	0.00
$\begin{array}{c} 616 \\ 602 \end{array}$	$\begin{array}{c} 61 \\ 62 \end{array}$	$\begin{array}{c} 23 \\ 27 \end{array}$	20,000	200,000	133	$33\frac{1}{2}$		105	1,896	0.95	0.96
002	62	21	30,000	300,000	134	$44\frac{1}{2}$		105	2,827	0.94	
0.10						controls					
649	$\frac{56}{6}$	231/2			128	431/2	300,000	33	32,940	10.98	10.98
648	56	$22\frac{1}{2}$			128	50			0	0.0	

^{*} Lambs exposed every other day.

infected controls. About 10 weeks after initial infection and 7½ weeks after the last exposure to larvae, single exposures of 300,000 larvae were administered to one member of each pair of previously infected lambs, and to one of the controls. This dose was selected because it normally produced severe, often fatal, infections in parasite-free lambs and kids. After the final exposure to larvae, the challenge-control lamb was separated from the uninfected lamb.

For the study of the development of resistance to this parasite on pasture, 3 parasite-free lambs similar in age and weight to those used in the experiment just described and 3 parasite-free kids approximately 6 weeks old were used. Two lambs and 2 kids were exposed to 30,000 larvae of S. papillosus (Table II). The remaining lamb and kid were not infected. The infected animals were transferred to a ¼-acre clean pasture of bluegrass, redtop, and mixed wild grasses. The uninfected control animals were put on a ½-acre clean pasture of the same type and quality as the pasture occupied by the principals.

Both pastures had been rested for a year, and the long drought of the previous year had aided in their parasitological decontamination. In addition all possible precautions were taken to prevent extraneous contamination of these areas before and during the course of the experiments.

In order to assure heavy contamination of the pasture occupied by the principals, approximately 10 pounds of fecal material containing large numbers of the eggs of *S. papillosus*, which were obtained from experimentally infected donor lambs, were distributed over the lot during the first week of the experiment. The infected animals were thus naturally exposed to larvae of *S. papillosus* which developed from the eggs distributed on the lot as well as from those passed in their own droppings. The latter were particularly numerous during the last $7\frac{1}{2}$ weeks of the 9-week period on the pasture. The 2 controls were not exposed to infection.

TABLE II.—Data on lambs and kids exposed to infection with S. papillosus on pasture during a 65-day period and subsequently challenged and their respective controls.

Animal No. L-Lambs K-Kids	Age and Weight at Time of Initial Infection		Initial Infec- tion (No. of Larvae)	Age and Weight at Time of Challenge		Challenge Exposure (No. of	Interval Between — Challenge	S. papillosus Recovered		
								No.	% of Larvae Admin-	Aver- age
•	(days)	(lb.)	· /-	(days)	(lb.)	Larvae)	Autopsy (days)		istered	%
L613	61	201/2	30,0001	126	30	300,000	26	2,900	0.88]	
$\substack{\textbf{L621}\\ \textbf{K282}}$	$\frac{60}{41}$	$\begin{array}{c} 25 \\ 15 \end{array}$	$30,000^{1}$ $30,000^{1}$	$rac{125}{106}$	$\frac{29}{24}$	300,000 300,000	$\begin{array}{c} 26 \\ 20 \end{array}$	$13,608 \\ 4,400$	4.10 (1.30 (2.9
K283	41	17	30,0001	106	$27\frac{1}{2}$	300,000	20	17,700	5.30	
$L603^{2}$	62	23	None	127	$31\frac{1}{2}$	300,000	26	82,338	27.50	48.05
$K280^{2}$	41	15	None	106	$28\frac{1}{2}$	300,000	14	205,850	68.60 ∫	10.00

Plus continuous exposure to infection on pasture after first 2 weeks.
 Controls: Both died of strongyloidiasis; others killed.

At the end of the ninth week each animal was tested for susceptibility or resistance to infection with S. papillosus as was done in the preceding experiment by a single exposure to 300,000 larvae (Table II).

RESULTS

Multiple Infections of Lambs in Pens.

The average weight gained by the pairs of infected lambs and their controls is shown in Figure 1A. There was a slight retardation in the growth of the infected

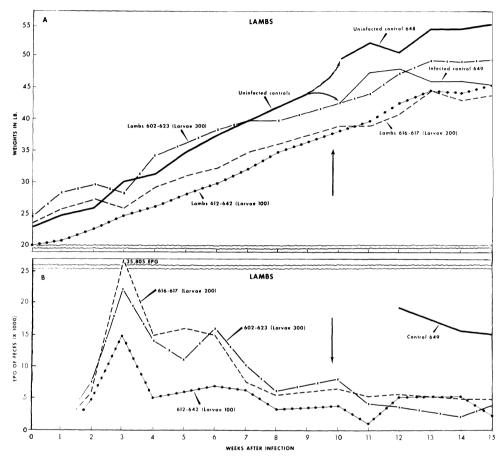


FIGURE 1. Multiple-infected lambs in pens. Arrows indicate when animals receiving initial infection were challenged and control was infected with 300,000 larvae. Larvae in thousands. A. Average weights of pairs of lambs similarly infected and controls. Control lambs after challenge shown separately; other pairs averaged after challenge because differences were minor. B. Average weekly egg counts for pairs of infected lambs. Egg counts first recorded for challenge-control lamb 2 weeks after challenge. As control 648 remained uninfected, there was no egg count from this animal.

animals before they were challenged. The pair receiving 100,000 larvae gained 17½ pounds, the pair receiving 200,000 gained 14¾ pounds, and the pair receiving 300,000 larvae gained 18¾ pounds, whereas the uninfected controls gained 23¾ pounds, or 5 to 9 pounds more than the principals.

The infected lambs after challenge either equaled or surpassed their unchallenged or uninfected controls in weight gains, with the exception of one pair. Challenged lamb 617 gained only 3 pounds during the postchallenge period, whereas its unchal-

lenged control, lamb 616, gained $9\frac{1}{2}$ pounds. The average weight gained by the challenged lambs was $6\frac{3}{4}$ pounds, and that by the unchallenged lambs was 7 pounds. The uninfected control, lamb 649, which was initially infected at the time the principals were challenged, gained only $2\frac{1}{2}$ pounds during the postchallenge period, compared with the $7\frac{1}{2}$ -pound gain of the remaining uninfected control lamb.

A slight-to-marked skin reaction at the inguinal site of larval application first appeared in all lambs on the fourth exposure to larvae 6 days after initial exposure. At this time pink areas were present in the inguinal region, and upon application of additional larvae a marked erythema developed. The erythema was particularly noticeable when the larvae were repeatedly applied to one area of inguinal skin, the rest remaining unexposed. After the sixth application of larvae, lamb 612 developed a slight erythema, which became more apparent 3 hours later. In this lamb the area of skin penetrated by the larvae was sensitive to touch and remained so for several days after the completion of the series of larval applications. In the other animals, however, only a slight reddening appeared, with no increase in intensity at the end of 3 hours. Urticaria was noticed after the seventh larval application in the 4 lambs receiving the smaller numbers of larvae. The wheals measured up to 3 cm in diameter and were accompanied by many pustules. Of the lambs exposed to a total of 300,000 larvae, no urticaria appeared, except in lamb 602 after the ninth larval application, and only varying degrees of erythema was seen in lamb 623 at any time. The sensitivity apparently was generalized, as erythema and/or urticaria appeared in both new and old exposure sites of the infected animals.

A marked erythematous reaction accompanied by urticaria was elicited by the challenge infections, the urticaria occurring within 2 hours after exposure. A day later the skin reaction was only slightly evident in lamb 642, and moderately persistent in lambs 617 and 623. No such reaction was observed in the parasite-free control lamb exposed for the first time to larvae of *S. papillosus*, or in any other lambs previously exposed to infection for the first time in the course of similar investigations.

The average numbers of eggs of *S. papillosus* per gram of feces passed by each pair of experimentally infected lambs and by the infected control lamb during each week of the experiment are recorded in Figure 1B. These data show that the eggs of this parasite appeared in the feces 9 to 10 days after the initial exposure to infection. The maximum number of eggs was passed approximately 3 weeks after the initial infection. The number of eggs then gradually decreased and was relatively small at the time the lambs were challenged.

The maximum number of eggs per gram of feces (EPG) passed by either of the lambs exposed to 100,000 larvae was 17,490; to 200,000 larvae, 62,520; and to 300,000 larvae, 29,490. These maxima occurred 22, 20, and 26 days after the initial infection, respectively, and were lower than those observed by the writer (1959) in a previously reported experiment in which the lambs received comparable numbers of larvae in single exposures. Maximum egg production occurred later in the lambs exposed to multiple infections than in lambs exposed to comparable single infections.

The numbers of worm eggs per gram of feces of the 3 previously infected lambs (642, 617, and 623) at the time they were challenged were 5,790, 9,060, and 6,300, respectively. The numbers passed at this time by the 3 lambs which were not challenged (612, 616, and 602) were 2,010, 4,200, and 9,720 EPG respectively. No

marked changes occurred in the number of eggs passed by the lambs after they were challenged with 300,000 larvae. The number of worm eggs passed by lamb 642 increased to only 10,800 EPG 3 weeks after challenge and then decreased to 4,800 EPG one week later. The number of worm eggs passed by lamb 617 did not increase until 5 weeks after challenge when only 10,000 EPG were recorded. The number of worm eggs passed by lamb 623 did not increase, but continued to decline until it was 750 EPG 4 weeks after challenge. The number of worm eggs passed by the unchallenged members of each infected pair of lambs continued to decrease to low levels, except that of lamb 602, which decreased only slightly to 7,440 EPG.

On the other hand, the number of eggs passed by challenge-control lamb 649, which received an initial dose of 300,000 larvae simultaneously with the challenged principals, increased to a maximum of 20,000 EPG 12 days after infection. The feces of uninfected control lamb 648 remained free from worm eggs throughout the experimental period. No abnormal stools were noticed in any of the animals during this time.

A slight decrease in hematocrit readings and hemoglobin values in the infected animals was noted during the first 9 weeks after initial larval exposure. The greatest hematocrit decrease, 36 to 25%, occurred in lamb 616 of the group given 200,000 larvae. The lowest hematocrit level was recorded the seventh week after the initial infection, and by the ninth week the hematocrit had risen to 30% and there was no subsequent decrease. The other member of the pair, lamb 617, maintained normal hematocrit levels during the same period. Lamb 616 also had the greatest decrease in hemoglobin, 3.1 g per 100 ml of blood. The other infected lambs displayed a decrease in hemoglobin of 0.6 to 2.7 g per 100 ml of blood. Thus, the hematocrit and hemoglobin values of the principals, except that of lamb 616, remained within normal limits throughout the experiment and were comparable to the uninfected controls prior to challenge.

Anemia did not develop in the infected lambs after they were challenged with 300,000 larvae, although a slight decline in the hematocrit reading from 29% to 27% occurred in lamb 617. However, lamb 649, which served as the challenge-control lamb, developed a moderate anemia after exposure to 300,000 larvae. The hematocrit declined from 34.5% to 26% and the hemoglobin from 10.8 to 8.2 g per 100 ml of blood in the 5-week period between infection and the termination of the experiment. The hematocrit and hemoglobin levels of the uninfected control, lamb 648, increased slightly during the same period.

None of the lambs in this experiment died, and none of the lambs receiving multiple doses, whether challenged or unchallenged, developed significant clinical symptoms, except the decreased rate of gain previously mentioned.

The lambs were killed 15 weeks after initial exposure to multiple infections, and 5 weeks after challenge. No pathology was noted in any of these animals. However, challenge-control lamb 649, which was given a single exposure of 300,000 larvae 5 weeks previous to autopsy, showed a generalized catarrhal enteritis throughout the duodenum and jejunum accompanied by erosion of the mucosa. This finding was similar to that previously observed in lambs subjected to single, massive invasions of larvae (Turner, 1955, 1959).

The numbers of worms, and percentages of larvae administered, which were recovered from the challenged and unchallenged lambs of each pair at autopsy were not large and only moderately higher in lamb 617, 1 of the 3 challenged lambs, than

in the unchallenged ones (Table I). These tabulated findings illustrate the immunizing action of the primary exposures to larvae.

Continuous Infections of Lambs and Kids on Pasture.

A slight retardation in weight gained by the principals as compared to the controls during their 9 weeks on pasture is shown in Figure 2. Infected lambs 613

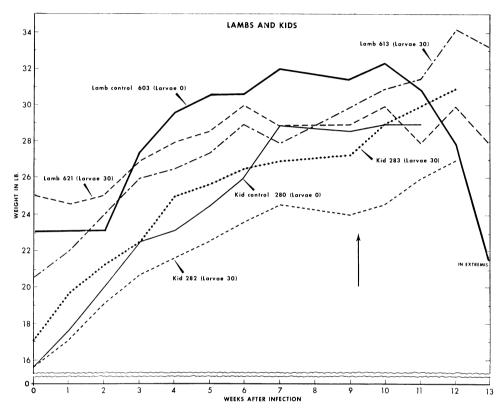


FIGURE 2. Weight data of individual lambs and kids infected on pasture. Arrow indicates when initial infection was challenged and controls were infected. Challenge-control kid 280 died 14 days after infection, and challenge-control lamb 603 killed in extremis 26 days after infection. Larvae in thousands.

and 621 gained 9½ pounds and 4 pounds, respectively, whereas the uninfected control lamb gained 8½ pounds. Infected kids 282 and 283 gained 9 and 10½ pounds, respectively, compared with 13½ pounds gained by the uninfected control. However, this trend was changed after challenge of the infected animals and initial exposure of the controls to 300,000 larvae. Four weeks after challenge, susceptible control lamb 603 had lost 10 pounds, whereas resistant lamb 621 lost 1 pound, and resistant lamb 613 gained 3 pounds. Susceptible kid 280 died 14 days after infection before any significant decrease in weight occurred, but it gained only ½ pound during this period in comparison to the 3 pounds gained by each of resistant kids 282 and 283.

Eggs of S. papillosus first appeared in the feces of all principals 9 days after infection (Fig. 3). During the prechallenge period of approximately 9 weeks, the

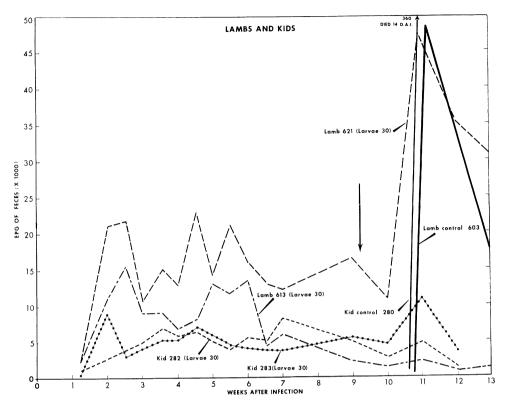


FIGURE 3. Worm egg counts of individual lambs and kids infected on pasture. Egg counts recorded for challenge-control lamb and kid during second week after challenge. Arrow indicates when animals receiving initial infection were challenged and controls infected with 300,000 larvae. Larvae in thousands.

lambs passed more worm eggs than the kids. The maximum numbers of eggs per gram of feces passed by lambs 613 and 621 were 15,750 and 23,100, respectively, and by kids 282 and 283 were 8,500 and 9,600, respectively. These peaks occurred 18, 32, 49, and 14 days, respectively, after infection. The number of worm eggs passed by these two lambs were relatively comparable to those of the lambs receiving 100,000 larvae, whereas those of the kids were roughly half this number. These maximum egg counts also were scattered over a period of 35 days, whereas those of the experimentally infected animals occurred over a period of 4 days.

Hematocrit percentages and hemoglobin levels decreased moderately in the infected lambs and kids during the first 9 weeks after the initial infection, and to a lesser extent or not at all in the uninfected controls. The hematocrit of lamb 613 decreased from 39 to 30% and of lamb 621, from 37 to 29%, whereas that of the uninfected control remained at 33%. The hematocrit of kid 282 decreased from 30 to 22%, that of kid 283 from 31 to 25%, and that of the control from 29 to 24%. The hemoglobin levels decreased 1.5 g per 100 ml of blood in lamb 613 and 2.1 g in lamb 621, whereas no significant change occurred in the control lamb. Greater decreases of hemoglobin occurred in the kids—3.7 g in kid 282, 2.6 g in kid 283, and 1.3 g in control kid 280.

At the time of challenge, 65 days after infection, the number of eggs of *S. papillosus* per gram of feces passed by the lambs and kids on pasture were as follows:

lamb 613, 2,280; lamb 621, 16,350; kid 282, 4,830; and kid 283, 6,330. Twelve days after challenge this number had increased significantly to 47,520 in lamb 621 and to 11,310 in kid 283. A week later the number of worm eggs had decreased below that recorded at time of challenge except in lamb 621, which maintained a high egg count until the experiment was terminated 4 weeks after challenge. The number of eggs per gram of feces passed by challenge-control lamb 603 attained a maximum of 48,540 12 days after initial exposure to 300,000 larvae and that of challenge-control kid 280 reached a maximum of 360,000 at the time of death (Fig. 3).

After the infected animals were challenged with 300,000 larvae, their hematocrit and hemoglobin levels did not decrease significantly except those of lamb 621. The hematocrit of this animal decreased from 29% to 24% and the hemoglobin declined 2.2 g per 100 ml of blood. In contrast, a moderate anemia developed in lamb 603 and kid 280, which served as challenge controls. The hematocrit of lamb 603 decreased from 33 to 24% and its hemoglobin declined 2.6 g per 100 ml of blood in the 4-week period subsequent to infection. During the 2-week period that kid 280 survived, its hematocrit declined from 24 to 16% and its hemoglobin level declined 4 g per 100 ml of blood.

Although various precautions were taken to exclude extraneous parasites from the experimental animals, various species of coccidia (Eimeria intricata, E. ninae-kohl-yakimovi, E. arloingi, and E. faurei) were found in all the lambs at various times after the 25th day on pasture. The kids apparently did not develop coccidial infections during their stay on pasture as determined by fecal examinations. Small numbers of eggs of Haemonchus contortus appeared in the feces of the lambs 63 days after they were placed on pasture, and a few eggs of Moniezia expansa were observed in fecal examination of lamb 621 late in the experiment.

Kid 280 died 14 days after exposure to 300,000 larvae. It was lethargic several days prior to death. Autopsy revealed peripheral congestion similar to pneumonitis in the lungs, fluid in the pleural cavity, ascites, and an enlarged gall bladder. The abomasum contained little food. Enteritis associated with thickened edematous areas confined to the duodenum was observed in the small intestine. Approximately 69%, or 205,850 threadworms, of the original dosage were recovered from this animal (Table II, K280). Of these, 4,500 were found in the abomasum; the rest in the small intestine. Many of these worms were in the fourth stage of development. The 2 challenged kids 282 and 283 were killed 20 days after challenge and a week after the challenge-control kid died. The organs of kid 282 revealed no gross pathology, and only 4,400 worms were recovered from the small intestine. In kid 283 there were a few petechiae in the upper diaphragmatic lobe of the left lung, possibly indicating recent passage of larvae through this region. The other organs appeared normal. A total of 17,700 worms were recovered, or approximately 4 times the number harbored by kid 282.

All the infected lambs (Table II) were killed on the same day, 26 days after challenge in the case of the principals (613, 621) and 26 days after infection in the case of the challenge control (603).

Autopsy revealed no gross pathology in lamb 613, and the carcass was in good condition. Only 2,900 S. papillosus, or less than 1% of the original infection, were recovered from the small intestine, and 6 H. contortus from the abomasum. Lamb 621 had ascites; otherwise, the findings at autopsy were normal. Approximately

13,608 *S. papillosus* and 70 *H. contortus* were recovered from this animal. Lamb 603 was moribund when it was killed. The necropsy revealed an enteritis, thickened duodenal mucosa, and fluid intestinal contents. All organs except the small intestine appeared to be normal. An estimated 82,338 worms were recovered from this animal. Although all animals were infected with various species of *Eimeria*, no coccidial lesions were noted in the intestines at autopsy. One tapeworm scolex was recovered from lamb 621.

DISCUSSION

These experiments show that a strong resistance to further infection with *S. papillosus* developed in the majority of the lambs exposed to immunizing infections in pens for a period of 20 days as well as in lambs and kids grazing for a period of about 2 months on a pasture that had been contaminated with the eggs and larvae of this parasite.

It is well known, however, that animals show considerable variation in the development of resistance to helminthic infection. Certain exceptions were also noted in these studies. Lamb 617, which was exposed to a total of 200,000 infective larvae given in multiple doses over a 20-day period, experienced a moderate exacerbation of infection when challenged, as determined by the number of worm eggs passed per gram of feces. However, some degree of resistance was established in this lamb, as only 8,028 worms (1.61% of the larvae administered) were recovered from it at autopsy, whereas 32,940 worms (10.98% of the larvae administered) were recovered from its challenge control. Another animal which apparently did not develop marked resistance to the same degree as the others was lamb 621 of the pasture experiment. This lamb after it was challenged passed a maximum of 47,520 EPG, whereas its uninfected control passed 48,540 EPG after receiving the single challenge exposure. The worms recovered from these two lambs, however, represented 4.1% and 27.5% of the number of larvae administered, respectively.

The data on the number of worm eggs passed, the changes in red cell volume, in the quantity of hemoglobin per 100 ml, and in body weight, as well as the autopsy findings, demonstrated that the immunizing infections greatly minimized the effects of a second or challenge exposure of lambs and kids to large numbers of infective larvae of *S. papillosus*. It appears significant that of the three susceptible challenge-control animals on pasture two died and one was severely affected. The reason that challenge-control 649 did not succumb to a number of larvae previously shown to be lethal is conjectural. It may be ascribed to individual variation in susceptibility or, perhaps, all of the larvae did not enter the skin. Nevertheless, the worm count at post mortem showed this animal to be more susceptible to the infection than the previously infected lambs.

These data support the results of certain other workers showing that an effective and persistent immunity develops in various hosts as a result of infection with other species of the genus *Strongyloides*. The development of resistance to reinfection with *S. stercoralis* in dogs has been reported by Sandground (1928), with *S. ransomi* in pigs by Enigk (1952a), and with *S. ratti* in rats by Sheldon (1937b). Chandler (1947) believed that helminths in the lumen of the intestine which feed on local tissues, such as *Strongyloides* spp., produce a localized, rapidly developing, powerful immunity. The development of such a localized immunity in the small intestine by repeated exposures to small numbers of larvae may explain why lambs were pro-

tected against massive challenge doses of infective larvae of S. papillosus. It seems probable that the larvae constituting the initial doses upon reaching the intestine and developing to maturity there excited an antigen-antibody reaction in the intestinal tissues, the antigen probably being some secretion or excretion of the parasite. immunity mechanism of S. papillosus may be similar to the "self-cure" phenomenon seen in sheep infected with various trichostrongylid nematodes, as noted by Stewart (1955). These nematodes live in the abomasum and intestine of sheep, and heavily infected animals will lose almost the entire population of adult worms if large numbers of infective larvae of the same, or closely related, species are ingested. infections of some species, however, according to Cameron (1956), may at times develop normally in sheep and cause fatalities. "Self-cure" appears to be due to a local abomasal or intestinal hypersensitivity caused by previous infections, which makes these habitats untenable for the adult parasites. This parallels the statement of Chandler (1953) that the intestinal immunization may be stimulated by older larvae or adult worms in the intestine. He also stated that in the case of nematodes which employ a parenteral phase of migration through the body, such as Strongyloides and Nippostrongylus, immunization may also be of the parenteral type and enhance intestinal resistance to the worms.

That *S. papillosus* can, under certain circumstances, cause a dermatitis in lambs was also demonstrated in the foregoing experiments. The erythema, urticaria, and increased sensitivity to touch that developed in the skin of the inguinal region of lambs after repeated applications of the larvae were similar to skin reactions of calves reported by Vegors (1954), and of rams and steers reported by Woodhouse (1948), which resulted from repeated cutaneous applications of larvae of this parasite. These authors reported a more intense reaction in cattle and sheep than that observed by the writer, which was probably due to the fact that they employed more larvae than the writer. These findings also paralleled those reported by Craig and Faust (1951) and Anon. (1955) on *S. stercoralis* in man and by Enigk (1952b) on *S. ransomi* of pigs, but were contrary to the observations of Sandground (1928), who stated that such sequelae were uncommon in dogs and cats reinfected with *S. stercoralis*.

SUMMARY

Immunizing infections against *S. papillosus* were induced in parasite-free lambs in isolation pens by cutaneous application of 10,000, 20,000, or 30,000 larvae at 2-day intervals for 20 days. Also, lambs and kids were initially infected by cutaneous exposures of 30,000 larvae each, and then grazed on a pasture where they were subsequently exposed to larvae of *S. papillosus* developing from eggs in feces spread on the area as well as from those in their droppings. None of these animals developed acute symptoms of strongyloidiasis. A strong resistance to further infection was demonstrated several weeks later by challenging one-half of the infected animals in pens and all on pasture with single, cutaneous exposures of 300,000 larvae, normally lethal for susceptible lambs and kids. Although the previously infected animals showed little effect of the challenge infection, 2 of the 3 parasite-free controls also exposed to 300,000 larvae at the time of challenge died.

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