OBSERVATIONS ON THE BIOLOGY OF *Ostertagia ostertagi* (STILES, 1892) RANSOM, 1907, IN THE DOMESTIC RABBIT

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1961

Submitted to the faculty of the Graduate School of
the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
May, 1965

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ACKNOWLEDGEMENTS

The author wishes to express his sincere gratitude to Dr. E. D. Besch, his major adviser, and Head of the Department of Veterinary Parasitology and Public Health, for his thoughtful guidance and advice throughout the course of this study and in preparation of this paper. Grateful acknowledgement is expressed to the committee members: Dr. D. E. Howell, professor and head of the Department of Entomology; Dr. R. R. Walton, professor of Entomology, for their constructive criticism of the thesis. Appreciation also is expressed to other members of the Veterinary Parasitology and Public Health Department who aided in any way during this study. The author wishes to thank the Oklahoma Agricultural Experimental Station and the College of Veterinary Medicine for providing experimental animals and research facilities.

Appreciation and gratitude are expressed to the author's brother, Dawood, for his encouragement during the course of graduate study. He wishes to thank the Iraqi Government for providing personal financial support.

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INTRODUCTION

In the science of parasitology, definition of the complex relations between host and parasite presents a constant challenge to the parasitologist. To meet this challenge, it is necessary that the worker be competent in the techniques of basic research and be able to use these techniques in his studies of biological associations. Recognizing the difficulties and the complexities associated with problems of pure science research, the writer decided to study the biology of Ostertagia ostertagi in domestic rabbit. Information was obtained concerning the details of host-parasite relationships, the morphology of developmental stages of nematodes and the gross pathology of lesions of helminth infections. Moreover, experience in helminthological research and in helminthological techniques was acquired.

There are seven species of the genus Ostertagia which have been reported from domestic ruminants in the United States. The economic importance and the damage caused by each species is difficult to ascertain because in most infections these parasites are usually associated with Haemonchus contortus or other gastro-intestinal nematodes. Ostertagia ostertagi, a pathogenic trichostrongylid worm of the abomasum of the ox, is widely distributed in the domestic cattle populations of the United States. In Oklahoma, it is considered to be more important than H. contortus.

Most of the recent advances in veterinary and medical parasitology would not have been accomplished without the use of small experimental

animals. This is especially true in studies of helminth infections of domestic animals for the definitive hosts often are expensive in price, costly to maintain, and difficult to examine. From a practical standpoint, a suitable experimental host is necessary to study the host-parasite relationships in order to determine more effective methods of control and treatment of parasitic diseases.

Alicata (1958) stated that the rabbit was not a very satisfactory host for Cooperia punctata. Wood and Hansen (1960) used male , white New Zealand rabbits as experimental hosts for the following nematodes: Cooperia punctata, C. curticei, Haemonchus contortus, Ostertagia circumcincta and Trichostrongylus colubriformis. Besch (1963) reported that the rabbit was a suitable host for C. punctata. No reports were found in the available literature of experimental infections of O. ostertagi in the various species of laboratory animals. Therefore, to acquire further information concerning the biology of O. ostertagi, the domestic rabbit was chosen as the experimental animal for this investigation. The objectives to be attained in this study were as follows:

1. To establish a patent infection of O. ostertagi in the domestic rabbit.
2. To determine the degree of infectivity of this nematode in rabbit.
3. To describe the development and the morphology of O. ostertagi in rabbit infections.
4. To illustrate and describe the gross lesions and macroscopic pathology of these infections.
5. To attempt to establish a rabbit adapted strain of O. ostertagi.

REVIEW OF LITERATURE

The literature review of Ostertagia ostertagi, (Stiles, 1892) Ransom 1907, will be confined to the objectives of this investigation as outlined in the introduction, and to the references in the available literature.

Ostertagia ostertagi is commonly called the medium stomach worm of cattle and is a nematode parasite of the abomasum of domestic ruminants. It was described by Ostertag (1890) from cattle in Germany and was named Strongylus convolutus. Many reports have been published concerning the taxonomy, biology, ecology and pathogenicity of this worm.

Stadelmann (1892) described the parasitic stages of S. convolutus collected from the stomach of cattle. He determined that the host becomes infected by ingesting the developed larvae; that the larvae penetrate and develop in the mucosa of the abomasum; and that the parasitic larval stages feed on blood. He concluded that there were only two parasitic larval stages, separated by a molt, in the life cycle of this parasite. He called these the first and second larval stages.

Stödter (1901) studied the life cycle of S. convolutus. He recovered larvae, mature worms, and larval exuviae in the nodules occurring in the mucous membrane of the abomasa of ruminants.

Stiles (1892) revised the genus Strongylus, determined that the specific name convolutus had been pre-occupied and named the species S. ostertagi after its discoverer. Ransom (1907) erected the genera Ostertagia, Cooperia and Nematodirus with brief description of new species. He stated the most important anatomical characters of the genus Ostertagia and briefly defined one of the species as Ostertagia ostertagi. Ransom (1911) redescribed the genus Ostertagia in detail and included a key for the species of Ostertagia. He stated also that S. ostertagi was a synonym of O. ostertagi.

Leiper (1908) united the genera Ostertagia, Haemonchus, Trichostrongylus and Cooperia into a subfamily Trichostrongylinae, which, in 1912, he elevated to the rank of family. Dikmans (1933) reported on the localization of O. ostertagi in the host animal. Skarbilovich (1935) studied the biology of the free-living larvae of O. ostertagi and the influence of external environmental factors on their development.

Porter and Cauthen (1946) determined the life cycle of this parasite in experimentally infected calves and stated that the prepatent period was 19 to 31 days. Threlkeld (1946) reported on the life history of this species, and described in detail the preparasitic and the parasitic stages in experimentally infected calves. He found that there were three ecdyses; one occurring outside the host and two occurring within the host. He stated the duration of the prepatent period was 23 days.

Douvres (1956) described the morphogenesis of the parasitic stages in experimentally infected calves. He stated that there were three ecdyses within the host rather than two as reported by Threlkeld (1946). In arriving at this conclusion, he considered the exsheathment of the parasitic third stage larva as a separate ecdysis.

Incidence and Pathogenicity of Ostertagia ostertagi

Ransom (1911) recorded the adult male of O. ostertagi at 6.5 to 7.5 mm and the adult female at 8.3 to 9.2 mm. Because of their smallness in size, these worms are overlooked on post-mortem examination and consequently their importance, incidence and distribution are not well known.

Stiles (1901) stated that, although the worm, O. ostertagi, is small, it was the chief factor of verminous disease in calves and steers in Texas. Baker (1937) reported that O. ostertagi was one of the most common nematode parasites of calves in New York State.

Porter (1942) pointed out that the majority of the animals that were examined in the southeastern part of the United States were infected with O. ostertagi. Threlkeld (1946) stated that the incidence of this parasite is apparently widespread and it has been reported from cattle in Australia, Argentina, New Zealand, Puerto Rico, Germany, England and several other countries. In the United States, O. ostertagi has been collected from cattle in California, Kansas, Louisiana, Alabama, Texas, Florida, Georgia, Illinois, Maryland, New York and Virginia.

Cooperrider et al. (1948) made a survey of the gastro-intestinal parasites collected from cattle in Oklahoma, and found that O. ostertagi was the most common species observed in the cattle examined.

Morgan and Hawkins (1949) reported that sheep and goats are occasional hosts, particularly when they are pastured with cattle or have followed cattle on range. Bell (1957) pointed out that ostertagiosis was a serious cattle parasite problem in North Carolina, and Bell, Turk and Galvin (1959) found that Ostertagia spp. were very common in cattle in northcentral and northeastern Texas.

Smith and Jones (1962) stated that brood cows, 2 to 9 years old, can be heavily infected with O. ostertagi, and they reported that 1,120,000 specimens were recovered from one of these animals. Most of the worms were in the larval and juvenile stages.

Krull (1963) pointed out that although this parasite normally inhabits the abomasum, it has been observed also in the initial part of the small intestine of cattle. He further stated that bison and antelope also are hosts, that the sheep is an occasional host, and that the horse is rarely a host. In Oklahoma this worm is probably more important than Haemonchus contortus.

From the information contained in the above reports, it is evident that this nematode species is a common parasite of the abomasum of domestic cattle in the United States.

Several papers have been published evaluating the pathogenicity of Ostertagia spp. in ruminant animals. Stadelmann (1892) reported that small nodules were formed in mucous membrane of cattle by the infective larvae of O. ostertagi. He found these nodules to vary in size from that of a pin head to that of a pea. Porter and Cauthen (1946) observed that gray nodules, each with a minute central cavity, were produced by the larvae of this species when they enter the gastric pits.

Threlkeld and Johnson (1948) reported that the most constant and predominant lesion in calves, following repeated doses of O. ostertagi infective larvae, was an erosion of the glandular epithelium of the abomasum. The eroded areas of the mucosa appeared as tiny white plaques on gross examination.

Sommerville (1953) observed that O. circumcincta infection in sheep, had a rather definite distribution in the abomasum. The worms

were found singly or in pairs in small nodules in the mucous membrane of the pyloric region and in the mucous membrane of the vulvulae terminalae around the cardiac orifice. Herlich (1956) reported that O. ostertagi also has a definite predilection for the mucous membrane of the folds of the fundus gland region of the abomasum.

Osborne, Batte, and Bell (1960) demonstrated that the third stage infective larvae invaded the gastric glands of the abomasal mucosa, and that these larvae were in the gastric glands as early as six hours after a single oral dose. They observed that gross lesions in the abomasum persisted for 46 days and submucosal oedema persisted for 25 days. Lapage (1962) stated that the infective larvae of O. ostertagi, after being ingested by the host, would penetrate the abomasal mucosa and cause the formation of small, circular, raised areas about 1 to 2 mm in diameter.

The Delayed Development Phenomenon

The delayed development phenomenon of nematodes in resistant hosts has been the subject of many reports in the recent literature. This phenomenon apparently occurs in host animals which have been exposed to infective larvae of certain nematodes and which have developed a resistance to these species. Upon re-exposure, the infective third stage larvae penetrate the mucosa, encounter adverse conditions in this environment and remain in the mucous membrane as an inhibited or dormant stage. Development of these larvae proceed to maturity when the micro-environmental conditions are optimum for the larvae to continue their development. Only those species that exhibit histotrophism are capable of undergoing a delay in development. Kotlan (1952) defined histotrophism as "migratory phenomena characteristic of nematodes larvae which

upon introduction into the alimentary tract, and their normal habitat, invade the mucosa in order to pass the third and perhaps also the fourth larval molt in that situation."

This phenomenon has been observed in many species of nematodes, e.g., Oesophagostomum columbianum, Cooperia curticei, C. onchophora, Haemonchus contortus, and H. placei.

Sommerville (1954) found that some of the larvae of O. circumcincta, which had undergone the third ecdysis, remained in the gastric pits and glands of a sheep for at least three months after infection.

Taylor and Michel (1953) reported that this inactive period or dormancy may provide a means of survival for the parasite, i.e., until a depression in the resistance of the host allows the parasite to develop to maturity.

Vegors (1958) examined eight bovine animals at necropsy after a barn confinement for 28 days and observed that the predominant stage of O. ostertagi in the collection was fourth stage larva. Michel (1963) reported that the development of O. ostertagi was inhibited in the early fourth stage in the presence of adult worms. This inhibition appeared to be reversible; larvae resumed their development after a reduction in the number of mature worms present in the abomasum.

Morgan, Parnell and Rayski (1951) were unable to determine whether the dormant larvae would overwinter in the host animal and, therefore, concluded that this phenomenon was apparently not important in the epidemiology of ostertagiosis. Sommerville (1954) stated that the significance of inhibited larvae in the epidemiology of ostertagiosis was not known and that the worms in the mucosa of the abomasum were not affected by anthelmintic treatment.

Many workers have reported that various components of the diet may affect the course of the larval development in a number of host species. Porter (1941) stated that the number of adult Haemonchus contortus that developed in calves fed on a milk diet were less in number and smaller in size than those recovered from calves fed on a diet of milk, hay and grain. All calves were given an equal number of infective larvae of H. contortus.

Rohrbacher (1957) stated that Trichostrongylus axei (bovine strain) was inhibited in its development to a greater extent in California white rabbits fed a diet of fresh green feed than in those fed a diet of a standard, commercial pelleted rabbit food. Rohrbacher et al. (1958) pointed out that a smaller number of Trichostrongylus axei and T. colubriformis were recovered from unweaned rabbits than from weaned rabbits.

Rabbits have been used by many workers as an experimental host for metazoa and protozoan parasites. Ortlepp (1939) established patent infections of T. colubriformis in rabbits. Wood (1958) and Wood and Hansen (1960) used male New Zealand white rabbits as experimental host for the following nematodes: Cooperia punctata, C. curticei, Haemonchus contortus, Ostertagia circumcincta and Trichostrongylus colubriformis.

Alicata (1958) stated that the rabbit was not a very satisfactory host for Cooperia punctata, but Besch (1963) reported that it was a suitable host for this parasite.

No reports were found in the available literature of experimental infections of O. ostertagi, in the various species of laboratory animals.

METHODS AND MATERIALS

Eight male and seven female New Zealand white worm-free rabbits, 7 to 13 weeks old, were used as the experimental hosts. These rabbits were kept in stainless steel rabbit cages. Each was fed daily a measured amount of a commercial pelleted feed. No supplemental green feed or antibiotics or drugs of any kind were given to these animals. Clean water was available at all times.

The rabbits were kept under conditions that reduced the possibility of reinfection. The wire mesh floor of the cages was kept free of the feces and the entire cage was cleaned with soap and hot water every two weeks.

A male Guernsey calf, three months old, was used as the source for Ostertagia ostertagi eggs. This animal had been infected with third stage infective larvae obtained from Louisiana Agricultural Experimental Station. Eggs that were collected with the feces were cultured to obtain infective third stage larvae.

A modified Cauthen sphagnum moss fecal culture technique was used throughout these experiments. As advocated by Whitlock (1960), sodium carbonate, 0.1 percent, was added to the feces to decrease the growth of fungus species which may have produced a detrimental effect on egg hatchability and larval growth. The amount of moisture needed to provide an optimum environment was the criterion used to determine the feces-sphagnum moss ratio. When water condensed on the sides of the culture container, the culture moss was considered to be too moist.

Sphagnum moss was thought to be a good substrate for larval development. This material also reduces the odor of feces, restricts the growth of bacteria and retains moisture over an extended period of time.

All fecal cultures were kept in covered buckets and were placed in the controlled temperature box at 28°C for 14 days. Cultures were maintained under optimum conditions to provide for the development of the maximum number of third stage larvae. Free-living nematodes, adults and developmental stages, were observed in nearly all fecal cultures. The number of Rhabditis sp. varied according to the amount of moisture contained in the culture moss; the number increased with the moistness of the sphagnum moss. The occurrence and growth of fungus species also was related to the moisture content of the cultures.

After 14 days of incubation, the cultured material was placed in warm tap water in a Baermann apparatus. The first water sample was withdrawn from the Baermann funnel after 8 to 12 hours. A second sample was withdrawn four hours later. It was noted that the majority of larvae collected from each culture were present in the first water sample.

Third stage larvae suspended in water were distributed to several Stender dishes and were concentrated by cooling the suspension for five to eight minutes, allowing the inactivated larvae to settle and siphoning off the excess fluid. At times, large amounts of moss debris were present in the samples obtained from the Baermann funnels. Larvae were caused to migrate from this debris by the light and the heat of a 75 watt bulb of a table lamp. This stimulation caused the third stage larvae to accumulate at the heated side of a Petri dish where they were collected easily with a pipette.

The number of the larvae given to each of the test animals was determined by a dilution counting method. A Stoll pipette was used to obtain a 0.15 ml aliquot sample from a thoroughly mixed water-larvae suspension. The larvae in the aliquot sample were placed in a watch glass and were counted under a stereoscopic microscope. Two aliquots were taken from each sample and the average was determined.

The total number of the larvae in each water suspension was calculated by multiplying the average number of larvae per aliquot by the number of 0.15 ml samples contained in the volume of the suspension.

Each rabbit of the test series received a known number of third stage infective larvae of O. ostertagi. The larval dose was given in water as a drench, and was administered with a dropping pipette. One rabbit was subjected to repeated doses of larvae over a period of 10 weeks; all other rabbits were infected with a single dose. The size of the larval dose ranged from 10,000 to 171,000 larvae. No difficulties were encountered in dosing procedure. It was noted that young rabbits were easier to drench by this technique than were older rabbits.

In the determination of the prepatent period, two methods were used to demonstrate eggs of the O. ostertagi in the fecal pellets of infected rabbits.

The sodium nitrate simple flotation technique was used to examine feces of rabbits during each of the three days prior to dosing and for each of the three days following dosing. This procedure was used to rule out the possibility of incidental parasitic infection. The technique that was used to examine the feces of infected rabbits involved suspending the feces in water, allowing the comminuted fecal material to settle and examining the sediment for eggs by using the sodium

nitrate flotation procedure. Fecal pellets of infected rabbits were examined twice daily from the eighteenth day post-infection until euthanasia.

All rabbits were euthanatized 28 days after infection by subjecting each to a continuous charge of 110-volt electric current. This method resulted in immediate death and necropsies were performed without delay. The digestive tract was removed with a minimum of handling and the digestive contents were retained in position by tying off the tract at four locations: at the cardia of the stomach; at the pylorus of the stomach; at the end of the first 12 inches of the small intestine; and at the end of the small intestine.

A complete parasitological examination was made of the contents and washings of the stomach and small intestine using the sedimentation-decanting technique. The collected material was placed in jars and fixed in 10 percent formal-saline.

The stomach of each rabbit was opened along the lesser curvature, the ingesta were removed and the mucous membrane was cleaned by washing and scrubbing with a fine brush. Line drawings were made to illustrate the pattern of the mucosal lesions. Photographs of each stomach were made using Kodak Super Panchro-Press, Type B, film. The number of worms in each collection was counted, the developmental stage of each was determined and a complete set of records was maintained.

To determine the developmental stages present in the mucosal lesions, one-half of each rabbit stomach was digested using the pepsin-hydrochloric acid digestion technique of Herlich (1956). The other half of each stomach was fixed in 10 percent formal-saline and was stored in jars.

The stomach-pepsin digestion preparation was maintained at 37°C for 4 to 6 hours, after which the digested material was diluted with physiological saline solution and was cooled in a refrigerator for 24 hours. The supernatant fluid was decanted and the sediment was examined for developmental stages.

Ostertagia ostertagi eggs, collected from fresh fecal material from the calf, were measured under a compound monocular microscope at 430 magnifications. All measurements were made with the aid of a calibrated ocular micrometer.

Heat killed third stage infective larvae, collected from calf fecal cultures, were measured under a compound microscope at 100 and 430 magnifications. All specimens, recovered from the stomach mucosal wash samples and from the nodules in the stomach mucosa were preserved in 10 percent formal-saline before they were mounted and cleared in lactophenol prior to examining for morphological details.

The Tri-simplex Microprojector was used to determine the measurements of all the developmental stages. However, the length of the esophagus, the width of the developmental stage, and the distance from the anus to the tip of the tail were measured under a compound microscope at 430 magnifications.

The exsheathment of the third stage larvae of O. ostertagi occurred when the larvae were subjected to a 0.05 percent sodium hypochlorite solution. Larvae were exsheathed in 3 to 15 minutes, average 10 minutes, at room temperature.

One rabbit, RN13, was drenched with 10,000 exsheathed larvae suspended in water. These larvae were examined before dosing, and were found to be alive and active.

OBSERVATIONS ON THE BIOLOGY OF *Ostertagia ostertagi* IN THE DOMESTIC RABBIT

Egg Characteristics

The eggs of *Ostertagia ostertagi* are ovate in shape, have a thin shell and are in the morula stage when passed in the feces of the infected animal. Measurements were made of 100 eggs collected from fresh feces of an infected calf, the length was in the range of 70 to 85.7 microns, average 78.8 microns; the width, 38.5 to 50.7 microns, average 43.1 microns. These measurements do not differ significantly from those reported for *O. ostertagi* by Skarbilovich (1935) and by Threlkeld (1946).

Third Stage Larval Characteristics

The third stage infective larvae, cultured in sphaguum moss at 28°C, developed in 64 to 70 hours. According to Skarbilovich (1935), third stage larvae develop in eight days in cultures kept at 27°C, while Threlkeld (1946) reported this developmental stage in cultures that were kept for five or six days.

Third stage larvae are ensheathed and are slender and cylindrical in shape. They taper more posteriorly than anteriorly. The majority of the larvae examined were characterized by the presence of 16 intestinal cells, a strongyliform esophagus, and a kinked sheath in the region of the posterior blunt tip.

Measurements were made of the length and width and of some anatomical parts of third stage larvae collected from calf feces-sphagnum moss

cultures and were compared with measurements of larvae reported by other workers. These data are summarized in Table I.

TABLE I

RESULTS SHOWING THE MEASUREMENTS OF THE THIRD STAGE INFECTIVE Ostertagia ostertagi LARVAE FROM EXPERIMENTAL CALF INFECTIONS+

Reference	Number of Larvae Measured	Length of Larvae*	Length of Esophagus*	Width at the Base of Esophagus*	Length of Sheath Beyond Tip of Tail*
Aljeboori 1965	100	855 (787.5-915)	169.5 (150-180)	25.62 (24.5-28)	60.9 (57-66.5)
Skarbilovich 1935	---	(713-780)	162	---	---
Threlkeld 1946	---	(850-900)	---	---	---
Keith 1953	---	(784-928)	---	24-28	55-75

*Figures in parentheses indicate the range of measurements.

+All measurements are in microns.

Examination of data presented in Table I shows that the gross measurements of third stage infective larvae of O. ostertagi used in these experiments were comparable to those measurements reported in the literature.

Parasitism involves a complex relationship between the host and the parasite. Numerous biological and physiological factors may influence this association, most of these are difficult to define. Whether a particular animal can serve as a host for a given parasite can be determined in a number of ways: The parasite may establish and develop to maturity

within the new host; the parasite may perish because of a host reaction or it may pass out of the host without further development; the parasite may exert an effect that will kill the host; the host may exert an effect that will stunt the parasite or cause it to fail to reach maturity, and egg production of the parasite may be affected due to the resistance of the host.

Natural resistance of the host may be influenced by many factors: The adequacy of the diet; the age and sex of the host; the physical state of the host, and inherited factors which may have an effect on the parasite. These factors, and probably others, determine the degree of the host-parasite relationship.

One of the main objectives of this study was to establish a patent infection of Ostertagia ostertagi in domestic rabbits.

Fifteen male and female, worm-free, white New Zealand rabbits were infected with larvae of O. ostertagi to determine whether the rabbit is an acceptable host for this nematode.

Prepatent and Patent Periods

The prepatent period of infection is the length of time that elapses between the invasion of the host by an infective larva and the recovery from that host of some new stage of the parasite. Normally this period is determined in infections of gastro-intestinal nematodes by the demonstration of eggs in feces of the infected animals. The duration of the prepatent period may be affected by physiological and immunological influences of the host. An increase in the duration of the prepatent period would indicate that the host-parasite relationship is not well adjusted, and may be indirect evidence that the potential host is not

very acceptable. However, failure to demonstrate a prepatent period in an experimental infection would indicate that the female parasite did not develop to maturity or that the female, although mature, did not produce eggs.

Typical Ostertagia eggs were observed in the fecal pellets of two rabbits, RN3 and RN5, and were demonstrated 26 and 53 days, respectively, after infection. Eggs were observed for only one day in flotation preparations of feces obtained from these two animals. These observations were the only evidence of patent infections that were obtained during this investigation. The limited data do not warrant the determination of the prepatent period for experimental infections of O. ostertagi in the rabbit.

The patent period of infection could not be determined for any of the experimental hosts. Although typical eggs were observed in the fecal pellets of two animals, the length of time that these eggs could be demonstrated was very short. No mature worms of O. ostertagi were collected from any of the infected rabbits including the two from which eggs were demonstrated in the fecal pellets. No specific explanation can be given for the absence of adult worms in the two patent infections. Many hypotheses can be advanced but none of these can be explained satisfactorily.

Parasitic Developmental Stages

Although no adult parasites were collected, numerous larval stages were recovered from stomach contents, mucosal washings and stomach mucosal digestant samples. Lesions were observed in the mucosa of the cardiac, fundic and pyloric region of the stomach of the infected rabbits. The number, position and macroscopic characteristics of these lesions will be described in a later section.

With the exception of two rabbits, fourth stage larvae were recovered only from the stomach mucosal washings and stomach mucosal digestant collections. The number of larvae collected from the stomach of each rabbit along with the percentage of the infective dose recovered as worms is summarized in Table II.

It is obvious from these data that a relatively small number of larvae established in each host regardless of the size of the infective dose. The number of the fourth stage larvae collected ranged from 1, in the rabbit that received 10,000 infective larvae, to 1771, in the rabbit that received 152,000 infective larvae. The percentage of the infective dose recovered as worms ranged from 0.01 percent to 1.28 percent. No trends were apparent nor was an optimum infective dose determined. The higher percentages of infection occurred, for the most part, in those animals which received the greatest number of infective larvae. More worms were recovered from the stomach mucosal wash samples than from the stomach mucosal digestant samples. It is evident that there were more worms on the mucosal surface of the stomach, 28 days after infection, than were in the mucosal lesions. The digestive tracts of the infected rabbits were examined immediately after euthanasia and the manner in which each was handled minimized the possibility of post-mortem migration or mechanical translocation.

Fourth stage larvae were recovered from the stomach contents of rabbit number 4 and rabbit number 11. These animals died 5 and 15 days, respectively, after infection. No developmental stages or mucosal lesions were observed in rabbit number 13 which was infected with 10,000 artificially exsheathed third stage larvae.

TABLE II

RESULTS SHOWING THE NUMBER OF FOURTH STAGE *Ostertagia ostertagi* LARVAE COLLECTED FROM RABBITS, 28 DAYS AFTER INFECTION

Rabbit Number	Sex	Age in Days	Size of Larval Dose	Number of Fourth Stage Larvae		Total Number of Worms	Percentage of Infective Dose Recovered
				Collected from Stomach Wash	Collected from Stomach Digestant		
RN1	M	53	10000	82	40	122	1.22
RN10	F	55	10000	1	--	1	0.01
RN8	F	49	25000	88	26	114	0.46
RN9	M	49	25000	13	2	15	0.06
RN11 +	M	49	25000	21	30	51	0.20
RN12	F	49	25000	23	--	23	0.09
RN2	F	73	50000	110	--	110	0.22
RN3	M	73	50000	21	--	21	0.04
RN6	M	63	50000	26	--	26	0.05
RN7	F	63	50000	71	28	99	0.19
RN14*	M	91	87000	495	400	895	1.28
RN5**	M	60	91300	668	104	772	0.85
RN4±	F	55	152000	1771	--	1771	1.17
RN15	M	91	171000	1045	282	1327	0.78
RN13 ‡	F	73	10000	--	--	--	--

+ Died after 5 days.

* Euthanatized after 15 days.

**Infected repeatedly.

± Died after 15 days.

‡ Infected with exsheathed third stage larvae.

The numbers of fourth stage larvae collected from male and female rabbits, 28 days after infection, are compared in Table III.

It is apparent, when these data are compared, that a greater number of worms was recovered from the male rabbits than from the females. The percentage of infective dose recovered as worms in male rabbits was in the range of 0.04 percent to 1.28 percent, while in female rabbits, 0.01 percent to 1.17 percent. Although these data were not subjected to statistical evaluation, male rabbits appear to be more susceptible to O. ostertagi infection than female rabbits. The large number of worms collected from rabbit number 4 can not be compared with the data from other female rabbits because this animal died fifteen days after infection.

Two species of intestinal adult worms of ruminants, Strongyloides papillosus and Cooperia punctata, were collected from approximately one third of the rabbits. The nematodes were recovered from the washings of the small intestine. These accidental infections resulted from larvae cultured from eggs in the feces of the calf infected with O. ostertagi. The prepatent period for S. papillosus infections in rabbits was in the range 10 to 13 days, average 12 days.

In order to determine the effect of the resistance of the host on the developmental pattern of the parasite, measurements were made of anatomical parts of some worms collected from these experimental infections. These data are summarized in Table IV and represent measurements made on fourth stage larvae that were in the early and late stage of development. Although the early fourth stage larvae predominated in all samples collected, no attempt was made to distinguish between the various age groups of fourth stage larvae when worms were selected for measurements.

TABLE III

RESULTS SHOWING THE NUMBER OF FOURTH STAGE Ostertagia ostertagi LARVAE COLLECTED FROM MALE AND FEMALE RABBITS, 28 DAYS AFTER INFECTION

Rabbit Number	Size of Larval Dose	Number of Worms Recovered	Percentage of Infective Dose Recovered
		MALES	
RN1	10000	122	1.22
RN9	25000	15	0.06
RN11	25000	51	0.20
RN3	50000	21	0.04
RN6	50000	26	0.05
RN14	87000	895	1.28
RN5	91300	772	0.85
RN15	171000	1327	0.78
		The range from 0.04 to 1.28	
		FEMALES	
RN10	10000	1	0.01
RN8	25000	114	0.46
RN12	25000	23	0.09
RN2	50000	110	0.22
RN7	50000	99	0.19
RN4	152000	1771	1.17
		The range from 0.01 to 1.17	

TABLE IV

RESULTS SHOWING THE AVERAGE MEASUREMENTS OF SOME ANATOMICAL PARTS OF FOURTH STAGE *Ostertagia ostertagi* LARVAE COLLECTED FROM RABBITS, 28 DAYS AFTER INFECTION*

Rabbit Number	Sex	Size of Larval Dose	Fourth Stage Larvae of O. ostertagi							
			Collected from Stomach Wash				Collected from Stomach Digestant			
			Length of Worm	Length of Esophagus	Width of Worm	Length Anus to Tip of Tail	Length of Worm	Length of Esophagus	Width of Worm	Length Anus to Tip of Tail
RN1	M	10000	1.37	0.3	0.03	0.07	1.20	0.26	0.02	0.06
RN10**	F	10000	1.19	0.3	0.03	0.07	--	--	--	--
RN8	F	25000	1.28	0.3	0.03	0.07	1.26	0.28	0.03	0.07
RN9	M	25000	1.40	0.3	0.03	0.07	1.27	0.29	0.03	0.07
RN11	M	25000	1.02	0.2	0.02	0.06	1.03	0.02	0.02	0.05
RN12	F	25000	1.36	0.3	0.03	0.07	--	--	--	--
RN2	F	50000	1.55	0.3	0.03	0.08	--	--	--	--
RN3	M	50000	1.33	0.3	0.02	0.07	--	--	--	--
RN6	M	50000	1.10	0.3	0.02	0.06	--	--	--	--
RN7	F	50000	1.80	0.3	0.03	0.07	1.28	0.27	0.03	0.07
RN14	M	87000	1.41	0.3	0.03	0.07	1.25	0.29	0.03	0.07
RN5	M	91300	1.62	0.3	0.03	0.07	1.25	0.28	0.03	0.07
RN4	F	152000	1.37	0.3	0.02	0.07	1.43	0.28	0.03	0.07
RN15	M	171000	1.35	0.3	0.28	0.07	1.19	0.26	0.03	0.07
RN13	F	10000	--	--	--	--	--	--	--	--

* All the measurements are in millimeters and are based on 10 worms selected at random.

**Measurements based on one worm.

From these data, it is apparent that the average length measurement for worms collected from the stomach mucosal wash was in the range of 1.02 mm to 1.80 mm while the average length measurement for worms collected from the stomach mucosal digestant was in the range of 1.03 mm to 1.43 mm. The size of the infective dose did not influence the average length of the worms measured, however, the position of the worm, on the mucosal surface or in the mucosal lesions, appeared to have had an influence on the length measurement.

The average measurements of the various anatomical parts were remarkably consistent and do not vary in respect to sex of host, size of larval dose or whether the worms were collected from the stomach mucosal wash or from stomach digestant samples.

Data showing the effect of sex of host on the development of O. ostertagi in rabbits, 28 days after infection, is presented in Table V.

TABLE V

RESULTS SHOWING THE AVERAGE LENGTH MEASUREMENTS OF FOURTH STAGE Ostertagia ostertagi LARVAE COLLECTED FROM MALE AND FEMALE RABBITS, 28 DAYS AFTER INFECTION

Rabbit Sex	Source of Worms	Number of Worms Recovered	Average Length (mm)	Range
Male	Stomach wash	69	1.35	0.93 to 2.80
	Stomach digestant	41	1.18	0.80 to 1.43
	Average - all worms	110	1.28	0.80 to 2.80
Female	Stomach wash	49	1.51	1.10 to 3.10
	Stomach digestant	17	1.28	1.10 to 2.10
	Average - all worms	66	1.46	1.10 to 3.10

From these data it is obvious that the average length measurements of fourth stage larvae, whether collected from the stomach mucosal wash

or from the stomach mucosal digestant, were larger in female rabbits than in male rabbits. That the fourth stage larvae grew to a greater length in female rabbits indicates that the sex of the host had an influence on the developmental pattern of the parasite. It can be further concluded from these data that the female rabbit is a more suitable experimental host than the male. However, these results are inconsistent with those presented in Table III which indicated, on the basis of the total number of worms collected, that the male rabbit was a more suitable experimental host animal. Due to the small number of host animals used and the small number of parasites obtained in each infection, these data were not subjected to statistical evaluation.

The average length measurements of worms collected from the stomach mucosal wash samples in male and female rabbits were consistently larger than the similar measurements of worms collected from the stomach mucosal digestant samples. The difference in the length measurement may be an indication of the increased growth of the fourth stage after these larvae leave the mucosal nodules.

Sex differentiation could not be made in the early fourth stage larvae, but, in a few instances, differences in the development of the genital structures were evident in the late fourth stage. The sexes could be distinguished on the basis of the width of the posterior end of the larvae which was broader in the male than in the female.

The morphological characteristics of the larvae, collected from rabbits, were observed and were found to be comparable to the larval descriptions reported by Douvres (1956). No diagonal striations on the cuticle were observed at the anterior end of the esophageal region as reported by Keith (1953) and Douvres (1956).

Fourth stage larvae also were recovered from the nodular lesions of the stomach at intervals of 15, 28 and 65 days after infection. No differences were observed in the morphology between any of these larvae and those collected from the stomach mucosal wash samples. The fourth stage larvae collected from the rabbit which died 5 days after infection apparently did not have time to develop and were smaller in size and averaged 1.02 mm in length. Ensheathed fourth stage larvae were observed among the worms collected from the stomach mucosal lesions of three rabbits. Apparently, development continues while the worms are in the nodules and a new sheath is formed prior to molting to the juvenile stage. This type of development of O. ostertagi was reported by Threlkeld (1946).

Description of Gross Lesions

The morphology of the rabbit digestive tract differs in many ways, from that of the calf. The rabbit stomach is simple, consisting of a single compartment and having three recognizable areas: the cardia, the fundus and the pylorus. The esophagus enters the stomach at the cardia and the contents leave the stomach, to the small intestine, through the pylorus. The fundic region makes up the bulk of the stomach. In the rabbit the cardiac opening is situated very close to the pyloric opening.

During this investigation, it was noted that the rabbit stomach was always full of ingesta even after the animal had been starved for 48 hours. The rabbit is a coprophagic animal and normally eats the fecal pellets that are produced during certain times of the day. Since the animals used were constantly hungry, this habit was intensified.

Ensheathed third stage infective larvae become parasitic after they are ingested, exsheathed and attempt to establish in a particular part of the alimentary tract of the definitive host. Sommerville (1957) reported

that larval exsheathment occurred after the ingested larvae were acted upon by some factor in the alimentary tract of the host and that ecdysis of these larvae was initiated in that part of the tract immediately anterior to where the adults were found. Thus ensheathed infective larvae of Haemonchus contortus, Trichostrongylus axei, and Ostertagia circumcincta, found as adults in the abomasum of sheep, were conditioned to exsheath while they were still in the rumen of the host. In the rabbit, an abnormal host, there is no part of the alimentary tract in which the infective larvae of O. ostertagi can be conditioned prior to establishment in the stomach. Larvae of O. ostertagi that are ingested by the rabbit not only must be conditioned, but must undergo exsheathment, prior to establishment in the stomach. This variation in the life cycle might explain why many ensheathed and exsheathed larvae were encountered in all the fecal samples that were examined, 24 hours after the rabbits were infected.

The degree and severity of the mucosal lesions produced by gastrointestinal nematodes may be influenced by a number of factors. Those that are important and should be taken into consideration are: the route of infection, the size of the larval dose, the sex and age of the host as well as the acceptability of the experimental host.

The gastric mucosa of all rabbit stomachs were examined, macroscopically, for evidence of lesions caused by developing larvae. Lesions observed were counted, the location of each in the mucosa was plotted on line drawings and the gross characteristics were compared to those described for the normal host.

Results showing the number of lesions observed in each stomach are summarized in Table VI. These data are compared to the size of the larval

TABLE VI

RESULTS SHOWING THE NUMBER OF LESIONS AND THE PERCENTAGE OF INFECTIVITY OF *Ostertagia ostertagi* IN RABBITS, 28 DAYS AFTER INFECTION

Rabbit Number	Sex+	Size of Larval Dose	Number of Lesions (Stomach)	Percentage of Infectivity	Number of Worms Recovered from Digestant
RN10	F	10000	40	0.4	--
RN9	M	25000	49	0.20	2
RN12	F	25000	86	0.34	--
RN8	F	25000	91	0.36	26
RN6	M	50000	112	0.22	--
RN3	M	50000	120	0.24	--
RN1	M	10000	165	1.6	40
RN7	F	50000	194	0.42	28
RN2	F	50000	210	0.42	--
RN5	M	91300	215	0.24	104
RN14*	M	87000	240	0.28	400
RN4 ‡	F	152000	382	0.25	--
RN15	M	171000	410	0.24	282
RN11±	M	25000	--	--	--
RN13++	F	10000	--	--	--

+ All rabbits were of New Zealand White Breed.

* Euthanatized 15 days after infection.

‡ Died after 15 days.

± Died After 5 days.

++Infected with exsheathed larvae.

dose (the resultant ratio is listed as the percentage of infectivity) and to the number of worms recovered from the stomach mucosal digestant samples.

These data indicate that the number of lesions occurring in the gastric mucosa increased with the size of the larval dose. The percentage of infectivity was in the range of 0.20 percent to 1.6 percent, average 0.40 percent. Although the number of lesions increased with the size of the larval dose, the percentage of infectivity was consistently low. The percentage for male rabbits was in the range of 0.20 to 1.6 percent and for the most part was very consistent regardless of the size of the larval dose. However, no reason can be given for the high number of lesions observed in rabbit number 1. The percentage of infectivity for female rabbits was in the range of 0.25 to 0.42, was fairly uniform regardless of the size of the larval dose and was consistently larger than the percentage obtained in the male rabbits. The persistence of these lesions in the females may have been due to a resistant reaction and not necessarily due to increased susceptibility of this sex.

It is apparent that in most infections that the number of lesions observed on the gastric mucosa was greater than the number of worms recovered from the stomach mucosal digestant samples. This discrepancy could be due to removal of some fourth stage larvae from the mucosal nodules during the initial examination of the digestive tract.

Rabbit number 14 was euthanatized 15 days after infection. The number of worms recovered in the digested material of this rabbit was greater than the number of lesions observed on the gastric mucosa. This indicates that a large number of worms, approximately 45 percent of the

total recovered, was still intimately associated with the mucous membrane 15 days after infection.

White circular nodules, sometimes plaque-like, each with a tiny central opening were observed to be situated in the mucosa of the stomach of each of the infected rabbits. The diameter of these nodules measured 1 mm to 2 mm, average 1.5 mm. The lesions were attributed to the reaction of the host to the developmental stage of O. ostertagi in the gastric mucosa. The majority of the nodules were singly distributed, however, confluent nodules were observed mainly in the cardiac region and in the mucosal line separating the fundus from the pyloric region. These confluent lesions measured, on the average, 3 to 5 mm in length. The distribution of these lesions is illustrated in Figures 1, 2, 4, 5 and 6.

Numerous lesions, pin head in size, were observed in the mucosa of pyloric region in rabbits numbered 4 and 15. These animals had received the largest number of larvae in the infective dose. The lesions observed in these rabbits are illustrated in Figures 3 and 7.

The distribution of the lesions in the gastric mucosa was observed to occur in the following frequency: the greatest number in the cardiac region, an intermediate number in the mucosal line separating the fundus from the pylorus and the least number in the fundus region. Many of the latter lesions were located on the rugae. The distribution of lesions in the stomach mucosae selected rabbit infections is illustrated in Figures 5 to 7.

Porter and Cauthen (1946) reported that gray nodules with a minute central cavity were produced by the infective larvae of O. ostertagi in the fundus region. Sommerville (1953) reported that lesions caused by

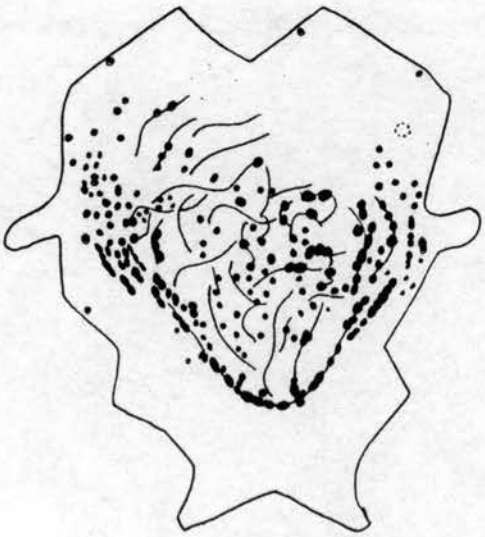

Fig. 1. Distribution of the nodules in the cardiac and fundic regions of the stomach of Rabbit number 5.

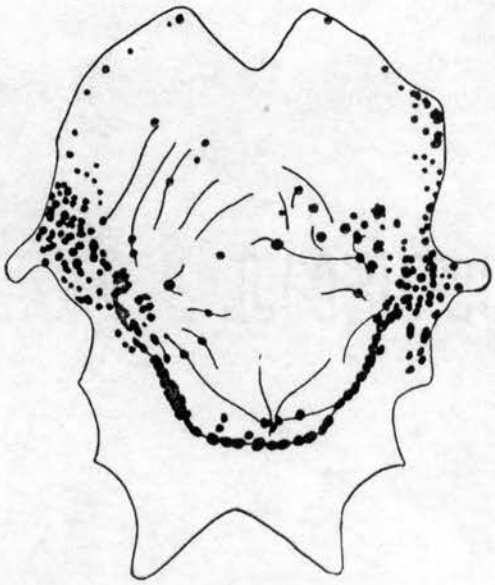

Fig. 2. Distribution of single and confluent nodules in the cardia and mucosal line of the stomach of Rabbit number 14

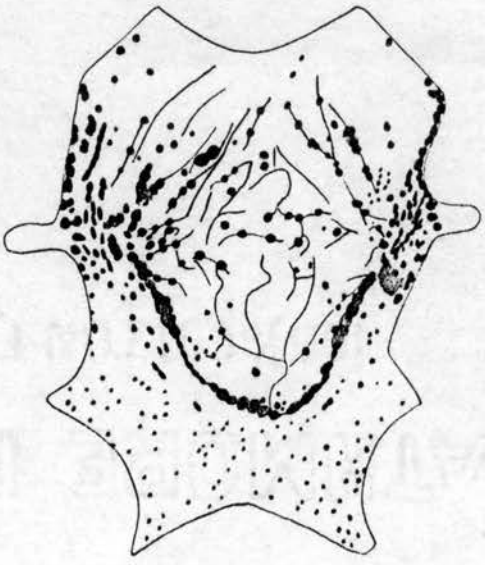

Fig. 3. Distribution of single and confluent nodules in the cardia, fundus, mucosal line and pylorus of the stomach of Rabbit number 15.

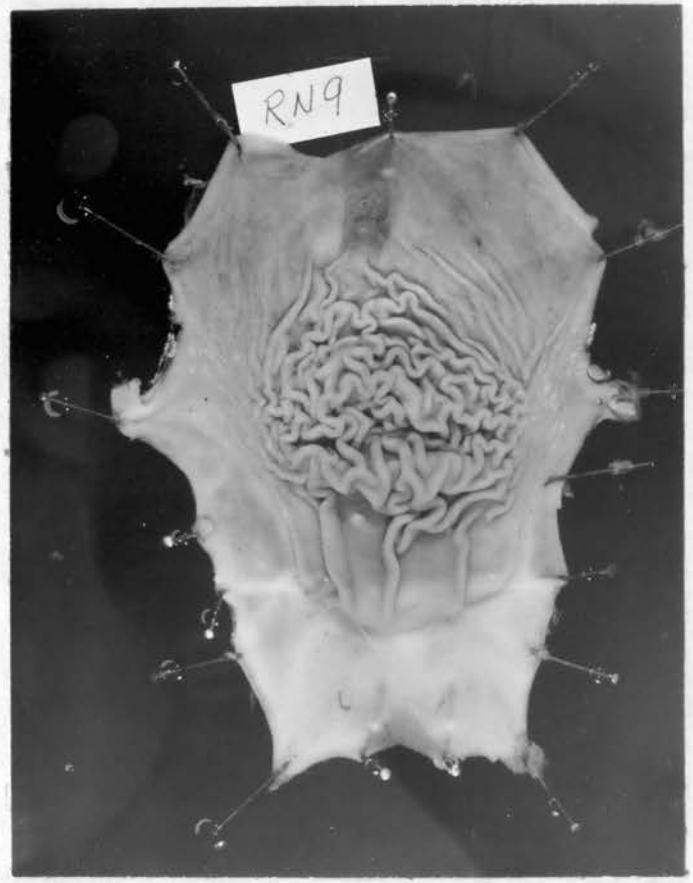

Fig. 4. Distribution of the small number of nodules in the cardiac region of the stomach in Rabbit number 9.

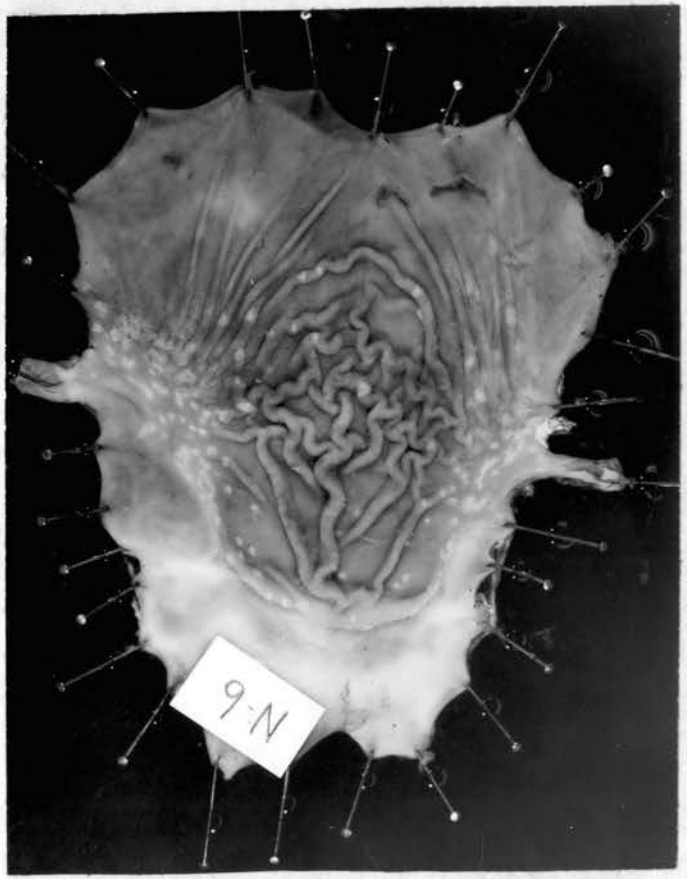

Fig. 5. Distribution of single lesions in the cardiac and fundic regions of the stomach of Rabbit number 6.

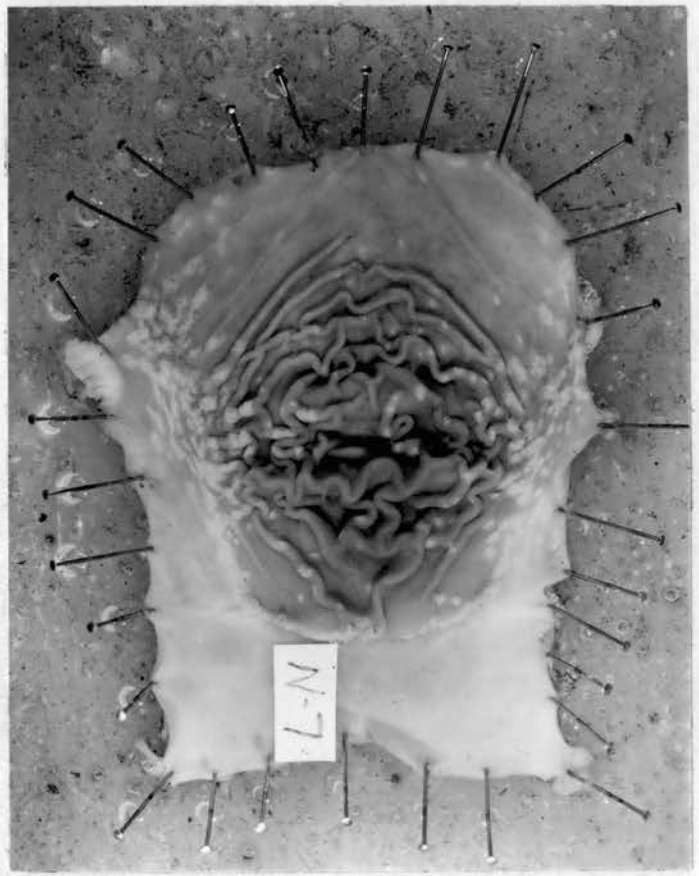

Fig. 6. Distribution of single and confluent lesions in the cardia, fundus, and mucosal line of the stomach of Rabbit number 7.

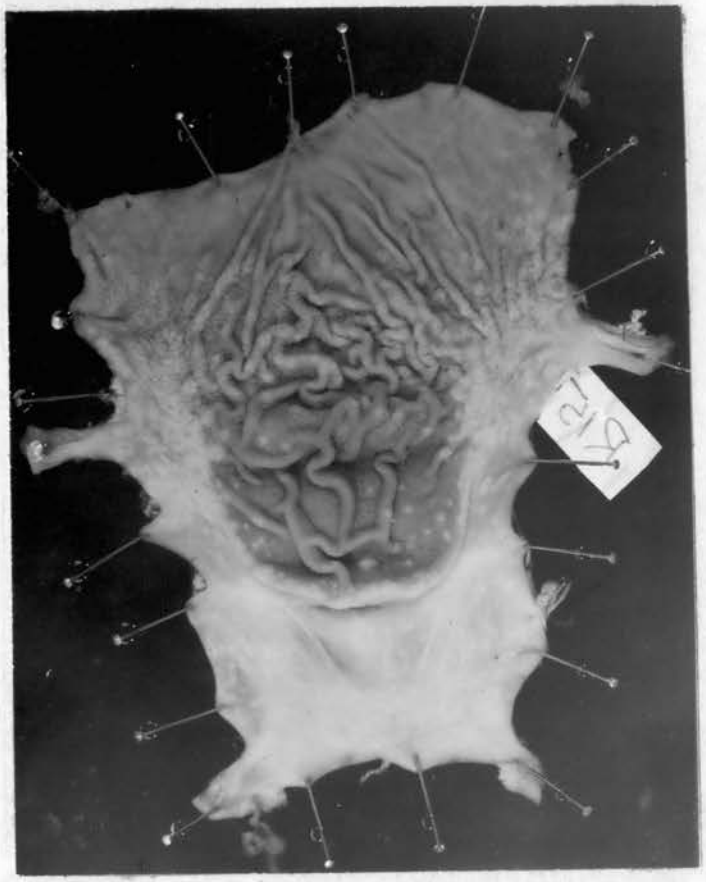

Fig. 7. Distribution of single and confluent lesions in the cardia, fundus, mucosal line and pylorus of the stomach of Rabbit number 15.

larvae of O. circumcincta had a definite distribution in the mucosa of the pyloric region and on the vulvulae terminalae around the cardiac orifice. Herlich (1956) stated that O. ostertagi larvae had a definite predilection for the mucosal folds of the fundus region of the abomasum. Osborne, Batte, and Bell (1960) demonstrated the lesions of O. ostertagi in calves. In these infections, they observed numerous grayish-white, circumscribed, raised plaques, about 2 mm in diameter, on and between fundus folds. They also stated that lesions in the mucosa of the pyloric region were not so numerous, and were less pronounced than those in the mucosa of the fundic region.

In the rabbit infections, the least number of lesions were observed in the fundus region and it is possible that the ingesta in each stomach may have been a barrier which prevented the infective larvae from reaching the mucosa of the fundus.

SUMMARY AND CONCLUSIONS

A limited number of articles concerning the incidence, pathogenicity and delayed development phenomenon of Ostertagia ostertagi was reviewed and discussed. Particular references were selected from the large number available and no attempt was made to complete a comprehensive review of the literature.

Experiments were completed to determine the acceptability of the domestic rabbit as an experimental host for O. ostertagi, a nematode parasite of the abomasum of the ox. Typical Ostertagia eggs were demonstrated for only one day in the fecal pellets of two rabbits. These limited data were the only evidence of patent infection and do not warrant the determination of a prepatent period for experimental infections in rabbits.

Results of data indicate that the rabbit, when kept on a reduced diet, has limited value as an experimental host for O. ostertagi. No mature worms of this parasite were collected from any of the rabbits infected during the investigation. Consequently, the patent period of infection could not be determined. Numerous fourth stage larvae were collected from the stomach contents, mucosal washings and stomach mucosal digestant samples. The early fourth stage larva was the predominant stage observed in all samples collected.

It was observed that a relatively small number of larvae established in each host regardless of the size of the infective dose. The number

of the fourth stage larvae collected ranged from 1 to 1771. The percentage of the infective dose recovered as worms ranged from 0.01 percent to 1.28 percent. More worms were collected from the stomach mucosal samples than from the stomach mucosal digestant samples. Fourth stage larvae were recovered from the contents of two rabbits that died early in the infection period.

A larger number of worms was collected from male rabbits than from female rabbits. The percentage of the infective dose recovered as worms in male rabbits was in the range of 0.04 percent to 1.28 percent, and in females, 0.01 percent to 1.17 percent.

The size of the infective dose did not influence the average length of the worms measured, however, the location of the worm, on the mucosal surface or in the mucosal lesions, appeared to have an influence on the length measurements. The average length measurements for worms collected from stomach mucosal wash samples was in the range of 1.02 mm to 1.80 mm, while the average length measurements for worms collected from the stomach mucosal digestant samples was in the range of 1.03 mm to 1.43 mm. The average length measurements of fourth stage larvae were larger in female rabbits than in male rabbits.

The morphological characteristics of the larvae, collected from rabbits, were found to be comparable to the larvae descriptions reported in the literature. Ensheathed fourth stage larvae were observed among those collected from the stomach mucosal lesions of three rabbits.

The degree of susceptibility of the rabbit to O. ostertagi was determined to be intermediate. Although patent infection did not occur, lesions were produced in the gastric mucosa of all infected rabbits with the exception of rabbit number 13 which received exsheathed larvae. The

number of lesions occurring in the mucosa increased with the size of the larval dose. The percentage of infectivity was in the range of 0.20 percent to 1.6 percent. The number of lesions that persisted in the gastric mucosa of female rabbits was consistently larger than the number of lesions occurring in male rabbits. The number of lesions observed on the mucosa of most rabbits examined was greater than the number of worms recovered from the stomach mucosal digestant samples.

White circular nodules, sometimes plaque-like, each with a tiny central opening were observed to be situated in the mucosa of the stomach of each of the infected rabbits. The diameter of these nodules measured ranged from 1 mm to 2 mm, average 1.5 mm. The lesions were attributed to the reaction of the host to the developmental stage of O. ostertagi in the gastric mucosa. The majority of the nodules were singly distributed, however, confluent nodules were observed mainly in the cardiac region and in the mucosal line separating the fundus from the pyloric region. These confluent lesions measured, on the average, 3 to 5 mm in length.

The distribution of the lesions in the gastric mucosa was observed to occur in the following frequency: The largest number in the cardiac region, an intermediate number in the mucosal line separating the fundus from the pylorus; and the smallest number in the fundic region.

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