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STUDIES ON CROSS-TRANSMISSION AND PATHOGENICITY OF *Haemonchus contortus* IN WHITE-TAILED DEER, DOMESTIC CATTLE AND SHEEP [□]

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Abstract: Experiments were conducted to compare the relative pathogenicity and infectivity of deer- and cattle-derived *Haemonchus contortus* for three hosts, viz., white-tailed deer, cattle and domestic sheep. Parameters evaluated for all animals were: general physical condition, basic hematologic values, fecal egg counts and parasite infectivity rates. Clinical signs attributable to *H. contortus* infections were not observed in any of the experimental animals. Deer harboring *H. contortus* burdens > 70 worms/kg body weight had decreased packed cell volume, hemoglobin and total serum protein values. Statistical analyses indicated there was not a significant difference ($P > .05$) in infectivity of deer-derived *H. contortus* in these hosts. No significant difference ($P > .05$) in infectivity for deer was noted between deer-derived *H. contortus* and cattle-derived *H. contortus*. Morphometric comparisons of helminths recovered indicated that parasites of deer and cattle origin were both compatible with the description for *H. contortus*. Results suggest that cross-transmission of *H. contortus* occurs between deer and domestic livestock.

INTRODUCTION

Nematodes of the genus *Haemonchus* are cosmopolitan parasites of the abomasum of cattle, sheep, goats and a variety of wild ruminants, and clinical disease caused by large numbers of these helminths is a well known syndrome manifest by severe anemia, hypoproteinemia, weakness and death.³⁰ In the past, the species of *Haemonchus* infecting cattle and sheep were considered distinct, i.e., *H. placei* and *H. contortus*, respectively; however, *H. placei* readily infected sheep, and *H. contortus* had a low infectivity for cattle.^{8,9,11,23,24} Presently, *H. placei* is considered a synonym of *H. contortus*.¹⁷ *Haemonchus contortus* in domestic ruminants has been postulated to be composed of several

strains, each adapted to a particular host-microclimate interaction.¹¹

Unfortunately, host or geographic strains are not limited to domestic animals. *Haemonchus contortus* s.l. (*sensu latu*) infections have been diagnosed in numerous wild ruminants in North America,^{1-5,7,28,34} and the epizootiologic potential of these hosts as reservoirs for infections in domestic livestock has been explored only for bighorn sheep (*Ovis canadensis mexicana*) and pronghorn antelope (*Antilocapra americana*).^{1-3,28} Of particular concern in this regard are white-tailed deer (*Odocoileus virginianus*) since: (1) infections of *H. contortus* in these animals are relatively common^{4,7,12-14,20-22,25} and (2) white-

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tailed deer are the most numerous and widespread of the big-game ruminants in North America.

This study was undertaken to compare the relative pathogenicity, infectivity and morphology of white-tailed deer-derived *H. contortus* for fawn and yearling white-tailed deer, lambs and calves. In addition, a trial was conducted comparing the pathogenicity, infectivity and morphology of white-tailed deer-derived and cattle-derived *H. contortus* for white-tailed deer fawns.

MATERIALS AND METHODS

Sources of Inocula. The deer-derived *H. contortus* were acquired and maintained as indicated in Figure 1. Approximately 3,500 adult female *H. contortus* obtained from the abomasum of a wild white-tailed deer from Glynn County, Georgia, were crushed and mixed with moist charcoal in a glass storage dish. The mixture was stored in the dark at room temperature (20-24 C) for 24 days, after which time 3,000 third stage larvae (L_3) were collected via a

Baermann apparatus. Two helminth-free, pen-raised deer were given 1,000 and 2,000 L_3 , respectively, *per os*.

After patency, fecal collections were made daily. Feces were cultured in moist vermiculite for 9 to 10 days, and infective larvae were harvested by the Baermann technique. Infective larvae were stored on moist filter paper at 4 C. A third pen-raised deer was infected with a portion (4,200 L_3) of the larvae. This animal and the two aforementioned "donor" deer provided infective material for all animals in trial 1. For infections, larvae stored on filter paper were recovered via the Baermann technique, pooled and the number of larvae estimated by counting ten 0.5 ml samples. Infective larvae of deer origin used in trial 2 were obtained from deer feces from trial 1. Infective larvae for trials 3 and 4 were obtained from donor deer infected with larvae from trials 2 and 3, respectively. Infective larvae used in trial 2 were stored in the same manner as those in trial 1. Infective larvae used in trials 3 and 4 were stored at 4 C in 50 ml bottles containing two 5 × 5 cm gauze pads.

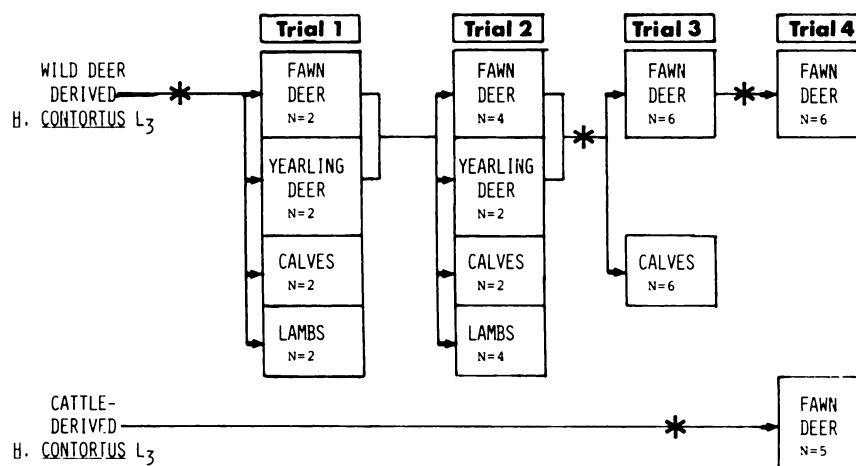


FIGURE 1. Sources of deer- and cattle-derived *Haemonchus contortus* used in trials 1-4. Asterisks represent donor deer or calf given deer- or cattle-derived *H. contortus*, respectively.

For trial 4 (Figure 1), cattle-derived *H. contortus* L₃ were obtained from Dr. J.C. Williams of the Louisiana Agricultural Experimental Station. Three thousand five hundred infective larvae were given to a helminth-free, pen-raised calf. Infective larvae for the cattle-derived inoculum were cultured from the feces of this "donor" calf and stored by the same techniques as the deer origin inoculum in trial 4. Cattle- and deer-derived *H. contortus* were prepared simultaneously for trial 4.

Animals. Orphaned white-tailed deer fawns were obtained from several state fish and wildlife agencies. Initially fawns were bottle fed, and a standard deer ration (University of New Hampshire deer diet)³² was offered *ad libitum* after 3 to 4 weeks. Two fawns in trial 4 were bottle fed throughout the experiment. Yearling deer used in trials 1 and 2 had been reared under similar conditions the previous year.

Pregnant ewes of mixed breeding were purchased and treated with Thiabendazole³³ to remove gastrointestinal parasites. The sheep were placed in concrete-floored, individual stalls where they were allowed to lamb. Ewes and lambs were maintained in isolation until lambs were weaned to the aforementioned deer ration. After weaning, lambs were held on concrete until placed on experiment.

Holstein calves used in trials 1, 2 and 3 were purchased at 2 to 3 days of age and placed in concrete-floored stalls where they were fed milk replacer until weaning. After weaning, calves in trials 1 and 2 were given deer ration and commercial range cubes³⁴ *ad libitum*, while calves in trial 3 were fed calf starter³⁵ and hay *ad libitum*.

Prior to infection, all animals were transferred to individual concrete-floored pens which were cleaned daily. Multiple fecal flotations were performed on each animal to detect inadvertent infection by gastrointestinal trichostrongyles.

Experimental Procedures. Four trials were conducted (Table 1 and Figure 1). Beginning 1 to 3 weeks prior to infection, blood samples were obtained from all animals at weekly intervals for hemograms. Average pre-exposure values of packed cell volume (PCV), hemoglobin (Hb) and total serum protein (TSP) were determined for each group of animals. Average weekly post-exposure values of PCV, Hb and TSP were then compared with the pre-exposure averages by the paired t-test.⁶ The average weekly percent changes in PCV, Hb and TSP for all deer infected with deer origin *H. contortus* were determined by comparison to pre-exposure means.

Feces were examined for *H. contortus* eggs once weekly until the second week postinfection (PI) and on three to five weekdays per week thereafter. Once infections were patent, eggs per gram of feces (EPG) were determined by a modified McMaster's technique.³⁰ In trial 4, average weekly EPG values for deer and cattle origin *H. contortus* were compared using the pooled t-test.⁶

Animals were killed 8 weeks PI in the first trial, 7 weeks PI in the second and 6 weeks PI in the third and fourth trials. At necropsy, the gastrointestinal tracts were removed and separated into abomasum, small intestine, cecum and large intestine. Each viscus was placed in a bowl, opened and the contents were washed in a 100 mesh screen. Gastrointestinal contents were pre-

³² Omnizole Suspension, Merck and Company, Rahway, New Jersey.

³³ Beef Pow'r Plus 20 cubes #8, Con Agra Inc., Omaha, Nebraska.

³⁴ Purina Calf Startina (Coarse) (G), Ralston Purina Co., St. Louis, Missouri.

served in 10% formalin, and *H. contortus* were counted by methods cited previously.²⁰ The abomasal wall was digested in a pepsin/HCl solution to recover larval nematodes.¹⁸ The percentage of the infective dosage recovered at necropsy was calculated, and these values were used to compare animal groups by the Wilcoxon two sample test,³¹ the Mann-Whitney test¹⁷ and the pooled t-test.⁶ The number of nematodes per kg body weight was determined for each deer. To study the relationship between parasitism and blood values, all deer infected with deer-derived *H. contortus* were placed into one or more of the following groups according to their *Haemonchus* burdens at necropsy, viz., <70, >70, >100 and >200 nematodes per kg body weight.

Body lengths were measured by placing parasites on microscope slides and projecting their images with an overhead projector at a distance which produced an 8× magnification. Tracings of the images were made and measured with a planimeter. Males were cleared in phenol, and the lengths of the spicules and the distances from the barb to the tip of each spicule were measured with an ocular micrometer in a compound microscope.

RESULTS

With exception of the calves in trial 1, patent infections were obtained in all experimental animals (Figures 2-4). Clinical signs attributable to *H. contortus* infections were not observed during trials 1-4. One fawn died of bacterial enteritis 3 weeks PI during trial 1, and one calf had severe scours during the first 2 weeks of trial 2. One fawn in trial 4 had bloody diarrhea 6 days PI, but the condition improved within 3 days.

Hematologic values did not change appreciably in deer during the course of trials 1 and 2, and hematologic values for calves and lambs remained within established normal values in trials 1-3.^{10,29}

In trial 3, appreciable changes in hematologic values occurred at week 4 PI in one fawn. This animal had reductions for PCV, Hb and TSP of -15.5, -5.2 and -1.5%, respectively. Deer in trial 4 infected with deer-derived *H. contortus* showed a

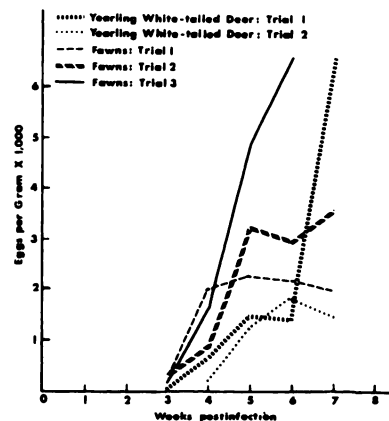


FIGURE 2. Average weekly parasite egg counts in feces of fawns and yearling white-tailed deer infected with a deer-derived *Haemonchus contortus*.

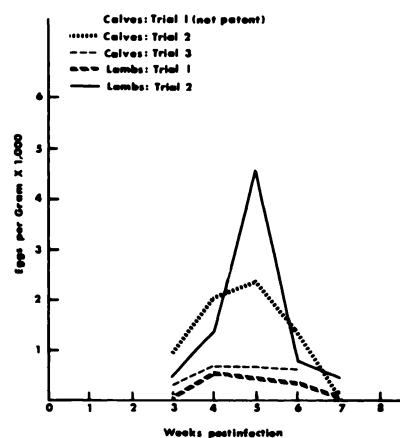


FIGURE 3. Average weekly parasite egg counts in feces of calves and lambs infected with a deer-derived *Haemonchus contortus*.

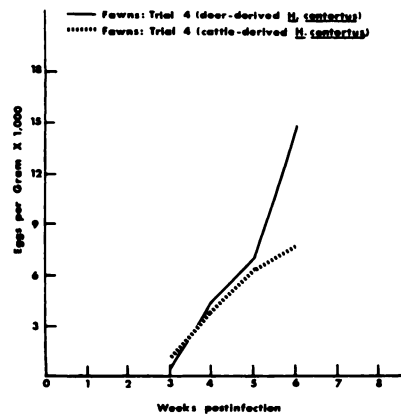


FIGURE 4. Average weekly parasite egg counts in feces of fawn white-tailed deer infected with either deer- or cattle-derived *Haemonchus contortus*.

significant reduction ($P < .05$) in PCV and Hb during weeks 3-6 PI and in TSP during weeks 2-6 PI compared to pre-exposure averages. Deer in trial 4 infected with cattle-derived *H. contortus* exhibited significant reductions ($P < .05$) in PCV during week 6 PI, in Hb during week 5 PI and in TSP during weeks 4-5 PI compared to pre-exposure averages.

Ranges for prepatent periods with deer-derived *H. contortus* in trials 1-3 were: fawns 21-28 days, yearling deer 22-28 days, calves 20-28 days and lambs 20-22 days. Ranges for prepatent periods in trial 4 fawns were: 19-32 days with deer-derived *H. contortus* and 19-21 days with cattle-derived *H. contortus*. Egg counts in trials 1-3 generally were greater where a higher dosage of infective larvae was given (Figures 2-4). Egg counts were somewhat erratic in deer; however, egg production was sustained longer in deer than in sheep or calves. In trial 4, there was no significant difference ($P > .05$) between the average weekly EPG values of deer infected with deer or cattle origin *H. contortus*. Egg counts were erratic in both groups, and egg production reached a higher level at week 6 PI in deer

infected with deer origin *H. contortus* (Figure 4).

Gross lesions attributable to *H. contortus* infections were not evident at necropsy. The number of *H. contortus* and percent of dose recovered from each animal are presented in Table 2. Very few ($< 1\%$) of the nematodes were immature. All measurements, including male and female body lengths, spicule lengths and the distances from the barbs to the tips of right and left spicules fell within the presently accepted ranges for *H. contortus*.¹⁷

In general, deer harbored greater numbers of the parasite than lambs or calves. In trial 4, deer infected with deer-derived *H. contortus* harbored greater numbers of the parasite than did deer infected with cattle-derived *H. contortus*. Parametric and non-parametric statistical comparisons of percentage infectivity between all deer and all calves or all deer and all lambs in trials 1-3 showed no significant difference ($P > .05$). Analyses of data from trial 4 revealed no significant difference ($P > .05$) in infectivity between deer infected with deer-derived *H. contortus* and deer infected with cattle-derived *H. contortus*.

DISCUSSION

Haemonchus contortus has been reported frequently from white-tailed deer populations in coastal plain regions of the Southeast.^{12,14,20,22} Although deer commonly are infected with other species of abomasal parasites,^{20,22} only *H. contortus* is considered a significant disease agent.^{12,16,21} A recent investigation revealed that fawns were particularly vulnerable to a syndrome of haemonchosis/malnutrition.¹² Diagnosis of this syndrome in wild deer populations has been hindered by lack of definitive guidelines to distinguish the threshold between pathogenic and non-pathogenic burdens of *H. contortus* in deer. Morbidity and mortality in anemic and debilitated deer with high burdens of *H.*

TABLE 1. Experimental design for infections of fawns, yearling white-tailed deer, lambs and calves with either deer-derived or cattle-derived *Haemonchus contortus*.

	Trial 1	Trial 2	Trial 3	Trial 4
	Deer-derived 6,460L ₃	Deer-derived 12,374L ₃	Deer-derived 20,000L ₃	Deer-derived 10,000L ₃
Fawn Deer				
No. Animals	2	4	6	6
Age	4-11 wks	4-19 wks	30-35 wks	11-13 wks
Diet	Milk+UNH-DD*	UNH-DD	UNH-DD	UNH-DD+Milk
Yearling Deer				
No. Animals	2	2	0	0
Age	12 mo.	18 mo.		
Diet	UNH-DD	UNH-DD		
Lambs				
No. Animals	2	4	0	0
Age	2-7 mo.	7-11 mo.		
Diet	UNH-DD	UNH-DD		
Calves				
No. Animals	2	2	6	0
Age	2-4 mo.	1-2 wks	12-15 wks	
Diet	UNH-DD+ Range Cubes**	Milk+UNH-DD	Calf Starter*** + Hay	

*University of New Hampshire deer diet¹²

**Beef Pow'r Plus 20 Cubes #8, Con Agra Inc., Omaha, NE

***Purina Calf Startina (coarse) (G), Ralston Purina Co., St. Louis, MO

TABLE 2. Numbers of *Haemonchus contortus* present at necropsy and percent of inoculum recovered.

	Trial 1		Trial 2		Trial 3		Trial 4	
	Deer-derived 6,460L ₃		Deer-derived 12,374L ₃		Deer-derived 20,000L ₃		Deer-derived 10,000L ₃ Cattle-derived 10,000L ₃	
Fawn Deer	130(2.0%)* 265(4.1%)		928(7.5%) 2264(18.3%) 2948(23.8%) 54(0.4%)		1885(9.4%) 6735(33.7%) 2008(10.0%) 848(4.2%) 625(3.1%) 1527(7.5%)		553(5.5%) 3740(37.4%) 2390(23.9%) 3565(35.7%) 1694(16.9%) 393(3.9%)	301(3.0%) 27(0.3%) 109(1.1%) 1542(15.4%) 701(7.0%)
Yearling Deer	669(10.4%) 811(12.6%)		308(2.5%) 1734(14.0%)					
Lambs	52(0.8%) 135(2.1%)		239(1.9%) 215(1.7%) 25(0.2%)					
Calves	2(0.1%) 4(0.1%)		1073(8.7%) 60(0.5%) 745(6.0%)		565(2.8%) 1254(6.2%) 2423(12.1%) 4565(23.3%) 41(0.2%) 845(4.2%)			

*Died at 3 weeks PI

contortus has been reported,²⁰ and a naturally occurring fatal case of haemonchosis was described in a wild fawn.²¹ Past studies have indicated that *H. contortus* burdens averaging 1,000 parasites or more per deer were sufficient to cause mortality in deer,^{12,14,20} but this figure was not absolute due to variables such as host size, age and other complicating factors.¹²

Evaluation of *H. contortus* burdens in terms of nematodes per kg body weight was proposed to reduce variability due to host size.¹² Recent field studies indicated that anemia and hypoproteinemia were correlated with this parameter. In wild deer, basic hematologic values (PCV, Hb, TSP) reached subnormal levels when *H. contortus* burdens averaged 75 parasites/kg body weight, and therefore this level was suggested as a guideline for pathogenicity.¹²

Hematologic profiles in this study coincided well with the above mentioned pathogenicity guideline. Collectively, deer infected with deer-derived *H. contortus* showed decreasing trends of PCV, Hb and TSP values at week 4 PI, but those with greater burdens were more adversely affected. A transition point was noted at week 4 PI, after which deer with burdens of <70 parasites/kg body weight showed restoration of PCV, Hb and TSP values (Figures 5-7). Hematologic parameters were not restored in deer with burdens of >70 worms/kg body weight, and the degree of anemia and hypoproteinemia corresponded well with the number of parasites/kg (Figures 5-7). Hematologic values in deer infected with cattle origin *H. contortus* had a similar pattern.

Evaluation of chronic effects of the above *H. contortus* burdens on deer was not feasible in these relatively short term infections. All animals used in this study were maintained on a high plane of nutrition (protein 16.8%, total digestible nutrients 90%)¹² and were free from other parasites. In contrast, wild deer often are

affected by malnutrition and other forms of parasitism concomitantly with haemonchosis.^{12,14,20,22} Consequently, wild deer may have greater anemia and debilitation than our experimental deer, and their health problems may be further

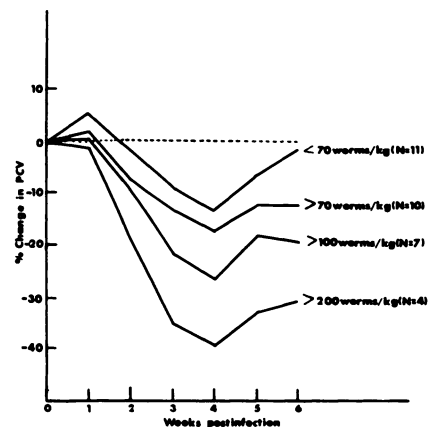


FIGURE 5. Percent change in PCV values in deer with deer-derived *Haemonchus contortus* burdens of <70, >70, >100, and >200 worms/kg body weight.

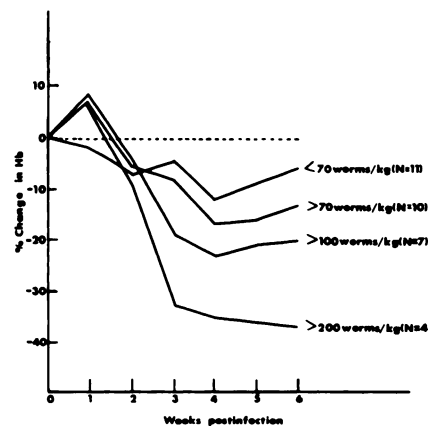


FIGURE 6. Percent change in Hb values in deer with deer-derived *Haemonchus contortus* burdens of <70, >70, >100, and >200 worms/kg body weight.

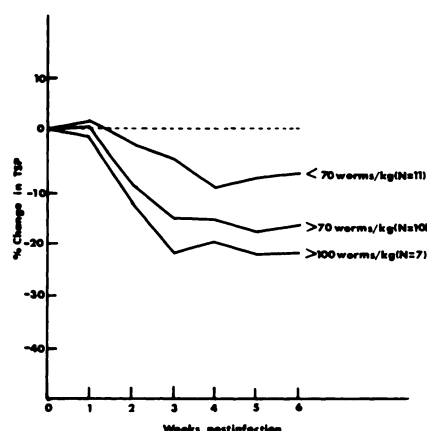


FIGURE 7. Percent change in TSP values in deer with deer-derived *Haemonchus contortus* burdens of <70, >70, and >100 worms/kg body weight.

compounded by other disease agents. We therefore conclude that infection intensities of over 70 parasites/kg body weight constitute a conservative guideline for pathogenicity.

The quantity of feces produced was much greater in lambs and calves than in deer, and for this reason, interspecific comparisons of egg counts per gram could not be made. Husbandry practices did not permit measurement of total fecal output and subsequent comparison of total egg production per host, which is regrettable when the ecologic consequences are considered. Thus, it was impossible to determine which host, if any, had the greatest potential for influencing environmental contamination with *H. contortus*. Results of this experiment did indicate, however, that calves and lambs infected with deer-derived *H. contortus* attain high EPG values which were comparable to EPGs previously described for *H. contortus* infections in these two hosts.^{2,24} Results also indicated that fawns infected with cattle-derived *H. contortus* had EPG values which were similar to those of deer in-

fectured with deer origin *H. contortus* (Figures 2-4).

Haemonchus contortus has been reported in intermingling populations of white-tailed deer and feral cattle,²² but there is little information on the amount of cross-transmission of *H. contortus* between these species. Although the parasite faunas of deer and cattle have been shown to be relatively distinct, *H. contortus* was one of the few helminths to occur in both hosts.²² In some reported cases, as cattle were removed from deer habitat, *H. contortus* disappeared from the deer population.²⁰ One factor which was thought to influence this disappearance was that *H. contortus* was considered to be evolving into "strains" which were adapted to specific hosts.²⁰

Results from this experiment, however, do not coincide well with the theory of well-adapted, host-specific "strains" of *H. contortus*. Several host-related factors have been shown to affect the infectivity of *H. contortus* in sheep and cattle, i.e., age,^{19,34} diet^{15,26} and genotype.^{27,35,36} The same likely is true for deer. In the experimental design of trials 1-3, there was no way to totally equate these variables or the possible effect of body weight differences between host groups; however, all subjects were adequately nourished immature animals which had no previous exposure to the parasite. Although the groups were small, the animals involved probably were representative of the thousands of deer, lambs and calves exposed to *H. contortus* by natural means.

Morphometric studies of the parasites recovered from the various hosts revealed that deer and cattle origin *H. contortus* were not morphologically distinguishable. All parasites recovered corresponded with the recent description of *H. contortus*,¹⁷ which tends to further discount the concept of host adapted "strains."

Recently, cattle and other domestic livestock were postulated to have been

important in the maintenance of *H. contortus* in deer in the Southeast.^{1,2} Domestic livestock were thought to influence the occurrence of *H. contortus* directly by cross-transmission of the parasite or indirectly through intensive competition for forage.^{1,2} Results of this study indicated that pathogenicity, infectivity and morphology of *H. contortus* in deer, cattle and sheep was independ-

ent of the host from which it was derived, and cross-transmission of *H. contortus* could occur between these hosts. Thus, *H. contortus* could be freely transmissible between deer and domestic livestock where they share common range, and this cross-transmission potential should be considered by wildlife managers and livestock producers when designing land management strategies.

Acknowledgments

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LITERATURE CITED

1. ALLEN, R.W., K.S. SAMSON and G.A. SCHAD. 1959. Cross-transmission of *Haemonchus* from pronghorn antelope to domestic sheep, with observations on the pathogenicity of this strain in lambs as compared with that of *Haemonchus* from domestic sheep. *J. Parasit.* 45 (4-Sect. 2): 47.
2. ———, ——— and G.I. WILSON. 1970. Partial immunity in sheep induced by *Haemonchus* sp. isolates from pronghorn antelope: effect of age of sheep host and chemical abbreviation of infections. *J. Parasit.* 56: 759-767.
3. ———, G.A. SCHAD and K.S. SAMSON. 1958. Experimental cross-transmission of two strains of *Haemonchus* from wild ruminants to domestic sheep, with observations of their pathogenicity as compared with *Haemonchus* from domestic sheep. *J. Parasit.* 44 (Sect. 2): 26.
4. BEAUDOIN, R.L., W.M. SAMUEL and C.P.A. STROME. 1970. A comparative study of the parasites in two populations of white-tailed deer. *J. Wildl. Dis.* 6: 56-63.
5. BECKLUND, W.W. and C.M. SENGER. 1967. Parasites of *Ovis canadensis canadensis* in Montana, with a checklist of the internal and external parasites of the Rocky Mountain bighorn sheep in North America. *J. Parasit.* 53: 157-165.
6. BHATTACHARYYA, G.K. and R.A. JOHNSON. 1977. *Statistical Concepts and Methods*. John Wiley and Sons, New York, NY. pp. 288-295.
7. BODDICKER, M.L. and E.J. HUGGHINS. 1969. Helminths of big game mammals in South Dakota. *J. Parasit.* 55: 1067-1074.
8. BREMNER, K.C. 1954. Cytological polymorphism in the nematode *Haemonchus contortus* (Rudolphi, 1803) Cobb 1898. *Nature* 174: 704-705.
9. ———. 1955. Cytological studies on the specific distinctness of the ovine and bovine "strains" of the nematode *Haemonchus contortus* (Rudolphi) Cobb (Nematoda: Trichostrongylidae). *Aust. J. Zool.* 3: 312-323.

10. COLES, E.H. 1974. *Veterinary Clinical Pathology*. 2nd edition. W.B. Saunders Co., Philadelphia, PA. 615 pp.
11. DAS, K.M. and J.H. WHITLOCK. 1960. Subspeciation in *Haemonchus contortus* (Rudolphi, 1803) Nematoda, Trichostrongyloidea. *Cornell Vet.* 50: 182-197.
12. DAVIDSON, W.R., M.B. MCGHEE, V.F. NETTLES and L.C. CHAPPELL. 1980. Haemonchosis in white-tailed deer in the southeastern United States. *J. Wildl. Dis.* 16: 499-508.
13. EMERSON, H.R. 1969. A comparison of parasite infestations of white-tailed deer from central and east Texas. *Bull. Wildl. Dis. Assoc.* 5: 137-139.
14. EVE, J.H. and F.E. KELLOGG. 1977. Management implications of abomasal parasites in southeastern white-tailed deer. *J. Wildl. Manage.* 41: 169-177.
15. FITZSIMMONS, W.M. 1969. Pathogenesis of the Trichostrongyles. *Helm. Abstracts* 38: 139-190.
16. FOREYT, W. and D.O. TRAINER. 1970. Experimental haemonchosis in white-tailed deer. *J. Wildl. Dis.* 6: 35-42.
17. GIBBONS, L.M. 1979. Revision of the genus *Haemonchus* Cobb, 1898 (Nematoda: Trichostrongylidae). *Systematic Parasit.* 1: 3-24.
18. HERLICH, H. 1956. A digestion method for post-mortem recovery of nematodes from ruminants. *Proc. Helm. Soc. Wash.* 23: 102-103.
19. MANTON, V.J.A., R. PEACOCK, D. POYNTER, P.H. SILVERMAN and R.J. TERRY. 1962. The influence of age on naturally acquired resistance to *Haemonchus contortus* in lambs. *Res. Vet. Sci.* 3: 308-314.
20. PRESTWOOD, A.K., F.A. HAYES, J.H. EVE and J.F. SMITH. 1973. Abomasal helminths of white-tailed deer in southeastern United States, Texas, and the Virgin Islands. *J. Am. vet. med. Ass.* 163: 556-561.
21. ——— and F.E. KELLOGG. 1971. Naturally occurring haemonchosis in a white-tailed deer. *J. Wildl. Dis.* 7: 133-134.
22. ———, ———, S.R. PURSGLOVE and F.A. HAYES. 1975. Helminth parasitisms among intermingling insular populations of white-tailed deer, feral cattle, and feral swine. *J. Am. vet. med. Ass.* 166: 787-789.
23. ROBERTS, F.H.S. 1957. Reactions of calves to infestation with the stomach worm, *Haemonchus placei* (Place, 1893) Ransom, 1911. *Aust. J. Agric. Res.* 8: 740-767.
24. ———, H.N. TURNER and M. McKEVETT. 1954. On the specific distinctness of the ovine and bovine "strains" of *Haemonchus contortus* (Rudolphi) Cobb (Nematoda: Trichostrongylidae). *Aust. J. Zool.* 2: 275-295.
25. ROBINSON, R.M., K.L. KUTTLER, J.W. THOMAS and R.C. MARBURGER. 1967. Theileriasis in Texas white-tailed deer. *J. Wildl. Manage.* 3: 445-459.
26. ROHRBACHER, G.H., D.A. PORTER and H. HERLICH. 1958. The effect of milk in the diet of calves and rabbits upon development of trichostrongylid nematodes. *Am. J. Vet. Res.* 19: 625-631.
27. ROSS, J.G., R.P. LEE and J. ARMOUR. 1959. Haemonchosis in Nigerian Zebu cattle: the influence of genetical factors in resistance. *Vet. Rec.* 71: 27-31.
28. SAMSON, K.S., R.W. ALLEN and G.A. SCHAD. 1964. Comparative pathogenicity in *Ovis aries* of homologous and heterologous strains of *Haemonchus* (Nematoda: Trichostrongylidae) from domestic and wild sheep. *J. Parasit.* 50: 421-426.

29. SCHALM, O.W., N.C. JAIN and E.J. CARROLL. 1975. *Veterinary Hematology*. 3rd edition. Lea and Febiger, Philadelphia, PA. 807 pp.
30. SOULSBY, E.J.L. 1968. *Helminths, Arthropods and Protozoa of Domesticated Animals*. Williams and Wilkins Co., Baltimore, MD. 824 pp.
31. STEEL, R.G.D. and J.H. TORRIE. 1960. *Principles and Procedures of Statistics with Special Reference to the Biological Sciences*. McGraw Hill Book Co., New York, NY. pp. 404-406.
32. THOMPSON, C.B., J.B. HOLTER, H.H. HAYES, H. SILVER and W.E. URBAN. 1973. Nutrition of white-tailed deer. I. Energy requirements of fawns. *J. Wildl. Manage.* 37: 301-311.
33. TRAINER, D.O. 1973. Caribou mortality due to the meningeal worm (*Parelaphostrongylus tenuis*). *J. Wildl. Dis.* 9: 376-378.
34. URGUHART, G.M., W.F.H. JARRETT, F.W. JENNINGS, W.I.M. MCINTYRE and W. MULLIGAN. 1966. Immunity to *Haemonchus contortus* infection: relationship between age and successful vaccination with irradiated larvae. *Am. J. Vet. Res.* 27: 1645-1648.
35. WHITLOCK, J.H. 1955. A study of the inheritance of resistance to trichostrongylidosis in sheep. *Cornell Vet.* 45: 422-439.
36. ———. 1958. The inheritance of resistance to Trichostrongylidosis in sheep. I. Demonstration of the validity of the phenomena. *Cornell Vet.* 48: 127-133.
37. WINKLER, R.L. and W.L. HAYES. 1975. *Statistics: Probability, Inference, and Decision*. Holt, Rinehart, and Winston, New York, NY. pp. 852-854.

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