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EVIDENCE FOR ARRESTED DEVELOPMENT OF ABOMASAL NEMATODES IN WHITE-TAILED DEER

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ABSTRACT: White-tailed deer (*Odocoileus virginianus*) obtained from Noxubee National Wildlife Refuge, Noxubee County, Mississippi (USA) during April ($n = 3$), June ($n = 5$), September ($n = 5$), and November ($n = 5$) 1989, were necropsied for counting and identification of adult and larval stages of abomasal nematodes. Fourth-stage larvae (L4) ($n \leq 25$) from each deer were randomly selected for measurement of total worm length and width. Adults of four worm species were found: *Mazamastrongylus odocoilei*, *M. pursglovei*, *Ostertagia mossi*, and *O. dikmansi*. There were no differences between months in adult male worm burdens for all species except *O. dikmansi* for which the April worm burden was greatest ($P \leq 0.05$). Overall, the length of L4 ranged from 929 to 4,361 μm. There were no significant differences ($P > 0.05$) between months in the mean length (1,334 to 1,532 μm) of L4. Except for low numbers of developing fourth-stage larvae (length >1,650 μm) in April (2.6%), June (7.4%), September (11.3%), and November (3.7%), worms were early fourth-stage larvae (EL4) or fully developed adults. Overall, the proportion of EL4 in individual deer ranged from 19 to 97%; in male ($n = 3$) and female ($n = 15$) deer the proportions of EL4 were 22.5% and 67%, respectively. The mean proportions of EL4 in female deer were 51.4% (April), 63.2% (June), 78.1% (September), and 74.7% (November), but there was no difference ($P > 0.05$) among the 4 months. In spite of the absence of a significant difference between months in proportions of EL4, we propose that the larger absolute numbers of EL4 in June and September was due to a seasonal arrested development that occurred among stomach worms of white-tailed deer. Further, based on the presence of higher numbers of EL4 and adults compared to developing fourth-stage larvae at all collections, we believe that arrested development is an integral part of the life cycle of these nematodes.

Key words: Abomasal nematodes, *Mazamastrongylus odocoilei*, *Mazamastrongylus pursglovei*, *Ostertagia mossi*, *Ostertagia dikmansi*, white-tailed deer, *Odocoileus virginianus*.

INTRODUCTION

Arrested development (inhibition, hypobiosis) is a mechanism which ensures survival of nematodes during unfavorable environmental conditions (Armour, 1970). In northern temperate regions of Europe and North America, *Ostertagia ostertagi* of cattle becomes inhibited apparently in response to cold conditions of winter; and in southern temperate climates *O. ostertagi* becomes inhibited in spring and summer in response to hot, dry conditions (Armour et al., 1969; Craig, 1979; Malone, 1983; Williams et al., 1983; Williams and Knox, 1987). Little research has been done to assess the occurrence and importance of arrested development of stomach worms of white-tailed deer. Preliminary studies indicated that the timing of inhibition in *Ostertagia* spp. and *Mazamastrongylus* (=*Ostertagia* = *Apteragia* = *Spiculopteragia*) *odocoilei* (Lichtenfels et al., 1992) of white-tailed deer in Ontario, Canada was similar to *O. ostertagi* with larval arrest occurring in winter (Baker and Anderson, 1975). Likewise, inhibition of development of stomach worms of deer in the southeastern United States could occur during spring as for *O. ostertagi* in cattle in the region (Williams, 1986; Couvillion et al., 1989), but this hypothesis has not been confirmed. Our objective was to determine whether there was evidence of seasonal arrested development among stomach worms of white-tailed deer from April through November.

MATERIALS AND METHODS

The study was done at Noxubee National Wildlife Refuge, Noxubee County, Mississippi, USA (33°15'N, 88°50'W). We tried to collect at least five adult deer during each of April, June, September, and November 1989. For the first three collections, deer were obtained at night by shooting; in November, abomasums were obtained from deer at a hunter check station. Ages of deer were determined by the method of Severinghaus (1949).

Abomasums were isolated and parasites were recovered, enumerated, and identified by the methods of Couvillion et al. (1982); in addition, abomasums were digested in tap water at 23 to 25 C for 16 to 20 hr and the mucosa was scraped to remove histotrophic larvae (Couvillion et al., 1989). Fourth-stage larvae (L4) ($n \leq 25$) from each deer were randomly selected for measurement of total worm length and width. Measurements were made with the aid of a drawing tube and electronic planimeter.

Data were subjected to an analysis of variance for a completely randomized design with subsampling using the Statistical Analysis System, General Linear Models Procedure (SAS Institute Inc., 1987). Where significant differences were found, the least significant difference (LSD) test (Steel and Torrie, 1980) was used to compare mean numbers of adult and larval worms and the least square means (LSM) test (SAS Institute Inc., 1987) was used to compare lengths and widths of larvae. Worm numbers of female and male deer were analyzed separately. Representative specimens of fourth-stage larvae of abomasal nematodes were deposited in the USDA Parasite Collection (accession No. 70328), Beltsville, Maryland (USA).

RESULTS

Eighteen deer were collected in April ($n = 3$), June ($n = 5$), September ($n = 5$), and November ($n = 5$). With the exception of two juvenile (<1 yr old) deer obtained in April all deer were adults (1 to 3 yr old). A single male deer was collected in September and two were collected in November; all other deer were females. Results are presented for female deer only unless otherwise noted.

Four nematode species were recovered: *Mazamastrongylus odocoilei, M. pursglovei, Ostertagia dikmansi,* and *O. mossi*; they had prevalences of infection of 100%, 60%, 27%, and 73%, respectively. For female deer, adult male worm numbers of *M. odocoilei* were significantly greater ($P \leq 0.05$) in June than in the other 3 months whereas numbers of *O. dikmansi* were significantly greater ($P \leq 0.05$) in April (Table 1). There were no differences ($P > 0.05$) between months in adult male worm numbers for the other two worm species. There was no difference between months in mean total adult worm numbers (Table 1).

Mean (±SE) numbers of L4 ranged from 1,623 (±1,298) to 4,430 (±1,124) and the number of L4 in individual deer from 880 to 7,720. Although there was no significant difference ($P > 0.05$) between months, the mean numbers of early fourth-stage larvae (EL4) increased gradually from April through September and then declined in November. Large numbers of EL4 were found in some deer during June and September (Fig. 1).

Measurements of length and width were done on 402 L4 obtained from female deer. Larvae that were ≤1,650 μm were considered to be EL4 whereas those >1,650 μm were categorized as developing fourth-stage larvae (DL4) (Baker and Anderson, 1975). The mean (±SE) lengths of L4 were 1,334 (±37) μm (April), 1,365 (±29) μm (June), 1,446 (±29) μm (September), and 1,532 (±36) μm (November). For individual deer, lengths of L4 ranged from 929 to 4,361 μm. There was no significant difference ($P > 0.05$) between months in the mean lengths of L4. Except for low numbers of DL4 (length > 1,650 μm) in April (2.6%), June (7.4%), and September (7.1%), most worms were either EL4 or fully developed adults.

Overall, the proportion of EL4 in individual female deer ranged from 36 to 97% ($\bar{x} = 67\%$). The mean (±SE) proportions of EL4 were 51.4% (±10) (April), 63.2% (±8) (June), 78.1% (±9) (September), and 74.7% (±10) (November). The proportion of EL4 in April was significantly lower ($P \leq 0.05$) than in September but the proportions of EL4 in June and November were not different ($P > 0.05$) from the other 2 mo (Table 1). For male

TABLE 1. Mean ± standard error and range (in parentheses) numbers of adult and fourth-stage larvae of abomasal nematodes and mean percent of total worm numbers represented by early fourth-stage larvae of adult female white-tailed deer collected from April to November 1989 in Noxubee County, Mississippi.

	Adult nematodes						Fourth-stage larvae				
	Males						Early fourth-stage larvae[a,b]		Developing fourth-stage larvae[b]		
Month	*M. odocoilei*[a]	*M. pursglovei*[b]	*O. dikmansi*[a]	*O. mossi*[b]	Females[b]	Total[b]	Total	Mean % of total worm burdens		Total fourth-stage larvae[b]	Total worms[b]
April (n = 3)[c]	187[d] ± 97 (50–330)	140 ± 69 (0–390)	53[d] ± 10 (20–80)	180 ± 69 (50–380)	893 ± 279 (250–1,790)	1,453 ± 419 (500–2,690)	1,580	51.4[d] ± 10 (36–72)	43	1,623 ± 1,298 (1,290–2,040)	3,076 ± 1,254 (1,790–4,230)
June (n = 5)	544[e] ± 75 (360–960)	64 ± 53 (0–200)	8[e] ± 8 (0–40)	144 ± 54 (0–320)	896 ± 216 (360–1,480)	1,656 ± 325 (960–2,680)	3,297	63.2[d,e] ± 8 (45–87)	263	3,560 ± 1,005 (1,000–7,400)	5,216 ± 972 (1,960–8,480)
September (n = 4)	150[d] ± 80 (40–160)	130 ± 59 (0–240)	0[e] ± 8 (0–0)	120 ± 59 (0–240)	440 ± 242 (120–760)	840 ± 363 (240–1,320)	4,117	78.1[e] ± 9 (52–97)	313	4,430 ± 1,124 (1,440–7,720)	5,270 ± 1,086 (2,760–7,960)
November (n = 3)	160[d] ± 97 (40–240)	0 ± 69 (0–0)	0[e] ± 10 (0–0)	27 ± 69 (0–80)	400 ± 279 (240–600)	587 ± 419 (280–880)	1,733	74.7[d,e] ± 10 (59–90)	0	1,733 ± 1,298 (880–2,480)	2,320 ± 1,254 (1,480–2,760)

[a] Means in the same column followed by the same superscript (d, e) were not significantly different ($P > 0.05$) by the least significant difference test.
[b] No significant difference ($P > 0.05$) between months by analysis of variance.
[c] Number of female deer evaluated.

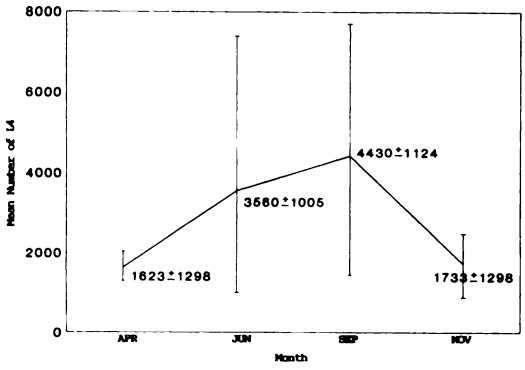

FIGURE 1. Changes in mean (±SE) numbers and ranges of fourth-stage larvae (L4) of abomasal nematodes of adult female white-tailed deer, 1989.

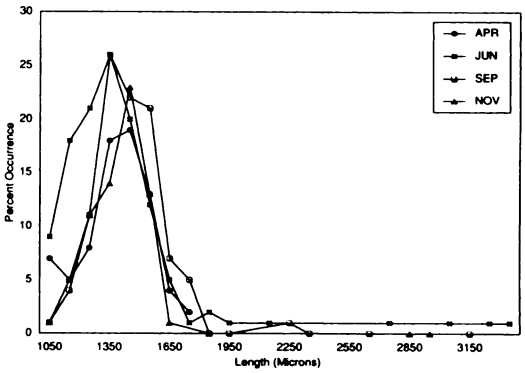

FIGURE 2. Distribution of lengths of fourth-stage larvae from adult female white-tailed deer.

deer the proportion of EL4 ranged from 19 to 30% ($\bar{x}$ = 22.5%).

DISCUSSION

This is the first report of seasonal studies of larval stages of abomasal nematodes of southeastern white-tailed deer. We found that larval trichostrongyles represent a significant proportion of stomach worm burdens of white-tailed deer. Morphometric characteristics of L4 (Fig. 2) were similar to those given by Baker and Anderson (1975). The worm populations of female deer were comprised principally of EL4 less than 1,650 μm and adult worms, but few (<7%) developing larvae. Baker and Anderson (1975) made a similar observation for white-tailed deer in Ontario, Canada. Michel (1974) considered such a distribution a cardinal sign of inhibition.

The proportion of larvae undergoing arrested development increased from April to September. Also, we infer from the presence of high and increasing numbers of EL4 from June to September (Fig. 1) concurrent with declining numbers of adult worms that seasonal arrested development occurred. Additional year-round studies would be needed to determine if larvae in arrested development continue to decline after November. Due to difficulties in obtaining adult deer, April data were determined from two juvenile females and one adult female. Further studies need to be done to determine any age effects on worm numbers.

Based on the consistent high proportion of EL4 in female deer over the 8-mo study period (Fig. 2), we believe that arrested development is an important and habitual aspect of the life history of one or several of the stomach worms of white-tailed deer. The reason for arrested development as related to survival of the worm population is unknown. In *O. ostertagi*, arrested development appears to be a mechanism for survival through periods of adverse climate. The cue for arrested development could be climatic; alternatively other factors such as host feeding activity could be involved. Accumulation of larvae in arrested development could be a method of maintaining the viability and transmission of stomach worms over long periods as with *O. ostertagi* of cattle (Williams, 1986). White-tailed deer are foragers in the southern U.S., but according to Yarrow and Jacobson (1986) deer spend more time browsing than grazing, minimizing exposure to infective larvae on grass. Thus, EL4 would develop to adults as needed to maintain egg shedding. Essentially, arrested development could be a mechanism of conserving the few infective forms acquired during minimal grazing activity. Although grass is a small part of the diet year round, acquisition of third-stage larvae alternately could be accomplished during ground

feeding in fall and winter when mast is an important foodstuff (Yarrow and Jacobson, 1986).

Because L4 cannot be identified to species, it was not possible to determine which of the four worm species present was undergoing arrested development. Typically, numbers of adult worms increase with the onset of development as burdens of L4 decrease and vice versa. A decrease in numbers of adult male *O. dikmansi* occurred coincident with increase in numbers of EL4 (Table 1). This observation alone, however, does not preclude the fact that EL4 were of one of the other three worm species.

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