DEVELOPMENT OF THE STOMACH WORM, OBELISCOIDES CUNICULI (GRAYBILL), IN LAGOMORPHS, WOODCHUCKS AND SMALL RODENTS

Authors: Measures, Lena N., and Anderson, Roy C.

Source: Journal of Wildlife Diseases, 19(3) : 225-233

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-19.3.225

Journal of Wildlife Diseases, 19(3), 1983, pp. 225–233

DEVELOPMENT OF THE STOMACH WORM, *OBELISCOIDES CUNICULI* (GRAYBILL), IN LAGOMORPHS, WOODCHUCKS AND SMALL RODENTS

Lena N. Measures and Roy C. Anderson
Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada

ABSTRACT: The parasitic development of *Obeliscoides cuniculi multistriatus* Measures and Anderson, 1983 was studied in New Zealand white rabbits (*Oryctolagus cuniculus*). Third-stage larvae exsheathed within 24 hr. The third molt occurred 3 days and the fourth 8–11 days post-infection. All worms were fifth stage 14 days post-infection. Males were mature at 16 days and copulation occurred in 15–16 days. Females were gravid at 18 days. The prepatent period was 16–22 days. The patent period was 61–118 days and males lived longer than females. All stages were found in the mucosa except the fifth which was found lying on the mucosal surface within a layer of mucus. Petechiae were the only lesions seen in experimentally infected rabbits. Patent infections of *O. c. multistriatus* were established experimentally in infected woodchucks (*Marmota monax*), snowshoe hares (*Lepus americanus*) and cottontail rabbits (*Sylvilagus floridanus*). Patent infections of *O. c. cuniculi* were established experimentally in snowshoe hares. Patent infections of *O. c. multistriatus* did not appear in experimentally infected HPB white (Swiss Webster) mice (*Mus musculus*), Wistar rats (*Rattus norvegicus*), H.O.R. F_1 Syrian hamsters (*Mesocricetus auratus*), H.O.R. F_1 smooth-haired guinea pigs (*Cavia porcellus*) and H.O.R. F_1 gerbils (*Meriones unguiculatus*).

INTRODUCTION

Obeliscoides cuniculi multistriatus Measures and Anderson, 1983 is a parasitic roundworm found in the stomach of snowshoe hares (Measures and Anderson, 1983a). Alicata (1932) described parasitic stages of *O. cuniculi* from experimentally infected guinea pigs but it is not apparent which subspecies of nematode he studied. Wallace (1942) infected a domestic rabbit with infective larvae of *O. cuniculi* obtained from a woodchuck. Worley (1963) gave domestic rabbits, guinea pigs, mice, rats and hamsters infective larvae of *O. cuniculi* obtained from a cottontail rabbit. Russell et al. (1966) compared experimental infections of *O. cuniculi* in domestic rabbits to that of *Trichostrongylus* and *Ostertagia* infections in cattle and sheep. Sollod et al. (1968) studied the parasitic development of *O. cuniculi* in domestic rabbits and determined the time of molt, location of worms in the stomach and the prepatent period. Russell et al. (1966) and Sollod et al. (1968) did not indicate the origin of *O. cuniculi* used for experiments.

Measures and Anderson (1983b) reported on the development of free-living stages of *Obeliscoides cuniculi multistriatus*. In the present study the parasitic development of *O. c. multistriatus* was followed in domestic rabbits. Larvae and subadults are described in detail and longevity of infections was determined. To determine whether patent infections could occur in other hosts, cottontail rabbits, snowshoe hares, woodchucks and small rodents were given infective larvae of *O. c. multistriatus*. Snowshoe hares were also given infective larvae of *O. c. cuniculi*.

Received for publication 18 October 1982.

MATERIALS AND METHODS

Maintenance of animals

New Zealand white rabbits, obtained through a commercial supplier (Maple Meadows, Acton, Ontario L7J 2L9, Canada), were housed in stainless steel rabbit cages with a steel mesh floor through which feces could fall. Snowshoe hares, cottontail rabbits and woodchucks were housed in similar cages. H.O.R. F_1 gerbils, HPB white (Swiss Webster) mice and H.O.R. F_1 Syrian hamsters were housed in plastic rodent cages. Wistar rats and H.O.R. F_1 smooth-haired guinea pigs were kept in stainless steel cages with a steel mesh floor. New Zealand white rabbits were given commercial rabbit ration (Shur-gain, Canada Packers Ltd., Toronto, Ontario L6T 1B9, Canada) medicated with sulfaquinoxaline. Snowshoe hares, cottontail rabbits and woodchucks were given a similar rabbit ration (United Co-operatives of Ontario, Mississauga, Ontario L5A 3A4, Canada). Other rodents were fed rodent laboratory chow (Ralston Purina Co., St. Louis, Missouri 63188, USA). All animals received food and water ad libitum and were housed with a 12-hr photoperiod at 20 C. Woodchucks were also given one apple each day.

TABLE 1. Experimental infection of woodchucks, snowshoe hares, cottontail rabbits and domestic rabbits with *Obeliscoides c. multistriatus* Measures and Anderson, 1983.

Host	Prepatent period (days)	Time of necropsy[a]	No. of worms recovered/ dose of larvae	Stage of worms recovered				Percent of total	
				L_3	L_4	Immature adult	Mature adult	Male	Female
Woodchuck 1	—	11	148/200	34	114	—	—	52	48
Woodchuck 2	32	34	44/200	—	—	—	44	86	14
Woodchuck 3	33	34	91/200	—	—	8	83	52	48
Woodchuck 4	36	37	124/200	—	10	20	94	40	60
Domestic rabbit	27	34	53/200	—	—	—	53	51	49
Snowshoe hare	29	36	20/200	—	—	—	20	5	95
Cottontail rabbit 1	25	25	2/200	—	—	—	2	50	50
Cottontail rabbit 2	20	21	3/200	—	—	—	3	33	67
Cottontail rabbit 3	—	25	3/200	—	—	—	3	100	—
Cottontail rabbit 4	25	25	1/200	—	—	—	1	—	100
Cottontail rabbit 5	—	23[b]	1/200	—	—	1	—	—	100
Domestic rabbit	22	23	17/200	—	—	—	17	41	59
Domestic rabbit	21	32	36/200	—	—	—	36	53	47

[a] Days post-infection.
[b] Died.

Infection of domestic rabbits

Obeliscoides cuniculi multistriatus maintained in domestic rabbits by continuous passage was originally obtained from a snowshoe hare collected near Lindsay, Ontario. Parasitic development was studied using 10 New Zealand white rabbits. Rabbits (6–8 wk old) were given approximately 500 infective larvae by gastric tubation. Infective larvae were counted by a dilution method. An uninfected control rabbit contained no worms when examined prior to the experiment. Rabbits were killed with Nembutal (Abbott Laboratories, Montreal, Quebec M5W 1V7, Canada) at 1, 3, 6, 8, 11, 14, 16, 18, 22 and 45 days post-inoculation and the stomach removed. Stomach ingesta from each rabbit were placed in warm saline (37 C) in a Baermann apparatus. The mucosa was scraped with a scalpel. The mucosa and the remaining stomach wall were placed in pepsin digests (7 ml concentrated HCl: 1,000 ml distilled water: 6 g pepsin) in separate Baermann apparatuses for 5–6 hr and worms were collected.

The longevity of infections was studied using six domestic rabbits each given 250 infective larvae. Rabbits were transferred to steam-cleaned cages twice weekly to prevent infection from infective larvae that had developed in feces. The prepatent period and the length of the patent period was determined by regular examination of feces for eggs. When eggs ceased to be passed the rabbits were killed and the worms counted. Feces were examined for eggs using zinc sulphate flotation.

Infection of other hosts

Three experiments were conducted to examine the host specificity of *O. c. multistriatus* and *O. c. cuniculi*.

Experiment I: Eight adult woodchucks trapped on the University of Guelph campus were killed and examined. None was infected with *O. cuniculi*. Feces of six young-of-the-year woodchucks trapped at the same location were examined for nematode eggs; none was found. These young animals, assumed to be uninfected, were used for the following experiment. Two male and two female woodchucks (Nos. 1–4) and a male domestic rabbit were each given 200 infective larvae of *O. c. multistriatus*. In addition, 200 larvae were given to a 1 yr old snowshoe hare bred and raised in the laboratory. Two woodchucks (1 male and 1 female) were kept as controls and were uninfected when examined 19 days after the beginning of the experiment.

Eight cottontail rabbits (4 males and 4 females) bred and raised in the laboratory and two domestic rabbits (1 male and 1 female) were each given 200 infective larvae of *O. c. multistriatus*. The prepatent period was determined by regular examination of feces. Seven uninfected cottontail rabbits raised in the laboratory were examined as controls; no *O. c. multistriatus* was found. At various times after infection animals were killed and examined for worms (Table 1).

Experiment II: Obeliscoides cuniculi cuniculi maintained in domestic rabbits by continuous passage was originally obtained from a cottontail rabbit collected in Ohio, USA. Six snowshoe hares (4 males and 2 females) bred and raised in the laboratory and one female domestic rabbit were each given 200 infective larvae of *O. c. cuniculi*. The prepatent period was determined by regular examination of feces. When infections were patent animals were killed and worms examined.

Experiment III: Two hundred infective larvae of *O. c. multistriatus* were given to each of three mice, three rats, three gerbils, three guinea pigs, three hamsters and two domestic rabbits. One hundred infective larvae were also given to an additional 11 gerbils. One of each species was killed as a control; no worms were found. Inoculated animals were killed various times post-inoculation and examined for worms.

Student's *t*-test was used to test significance of measurements of adult worms from woodchucks,

TABLE 2. Number and stage of *Obeliscoides c. multistriatus* Measures and Anderson, 1983 recovered from infected domestic rabbits given approximately 500 infective larvae.

Time of necropsy*	Total no. of worms recovered	Stage of worms recovered (% of total)				Percent of total worms recovered	
		Third stage	Fourth stage	Immature adult	Adult	Male	Female
1	330	330 (100)				—	—
3	412	412 (100)				—	—
6	512	9 (2)	503 (98)			46	54
8	456		456 (100)			41	59
11	301	1 (0.3)	244 (81)	56 (19)		41	59
14	348		3 (1)	345 (99)		52	48
16	46			20 (43)	26 (57)	57	43
18	122			11 (9)	111 (91)	60	40
22	129			2 (2)	127 (98)	83	17
45	3				3 (100)	100	—

* Days post-infection.

snowshoe hares, cottontail rabbits and domestic rabbits.

Examination of O. cuniculi: Worms were examined live or fixed in hot glycerin alcohol (1 part glycerin to 9 parts 70% alcohol). Worms were cleared by allowing the alcohol in the fixative to evaporate slowly leaving the worms in glycerin. The synlophe was studied as described in Measures and Anderson (1983a). Specimens of various stages have been deposited in the National Museum of Natural Sciences, Invertebrate Zoology Division in Ottawa, Ontario, Canada K1A 0M8 (No. NMCIC(P) 1983-0010).

RESULTS

Development in domestic rabbits

One to 3 days: All worms recovered from two rabbits were third-stage larvae (Table 2). On day 1 worms were exsheathed and were found within the mucosa. On day 3 most larvae were molting and were within the mucosa.

Six to 11 days: Most larvae recovered 6 days post-infection were fourth-stage larvae (Table 2). Worms were found within the mucosa. Petechiae were seen on the stomach mucosa.

All larvae were in the fourth stage 8 days post-infection. Most male and a few female fourth-stage larvae had begun to molt. Petechiae were observed on the mucosa of the rabbit killed at 8 days.

Eleven days post-infection most worms were molting fourth-stage larvae. Some were immature adults (early fifth stage).

Fourteen to 45 days: Almost all worms recovered at 14 days were immature adults (Table 2). A few molting female fourth-stage larvae were recovered. A completely developed bursa was present in males but spermatozoa were not observed in the reproductive tract. Petechiae were observed on the stomach mucosa 14 days post-infection.

At 16 days immature and mature worms were present. Spermatozoa were observed in the reproductive tract of males and in the proximal part of uteri of females. Females were not gravid. Spicules were not fully sclerotized. Petechiae were observed on the stomach mucosa 16 days post-infection.

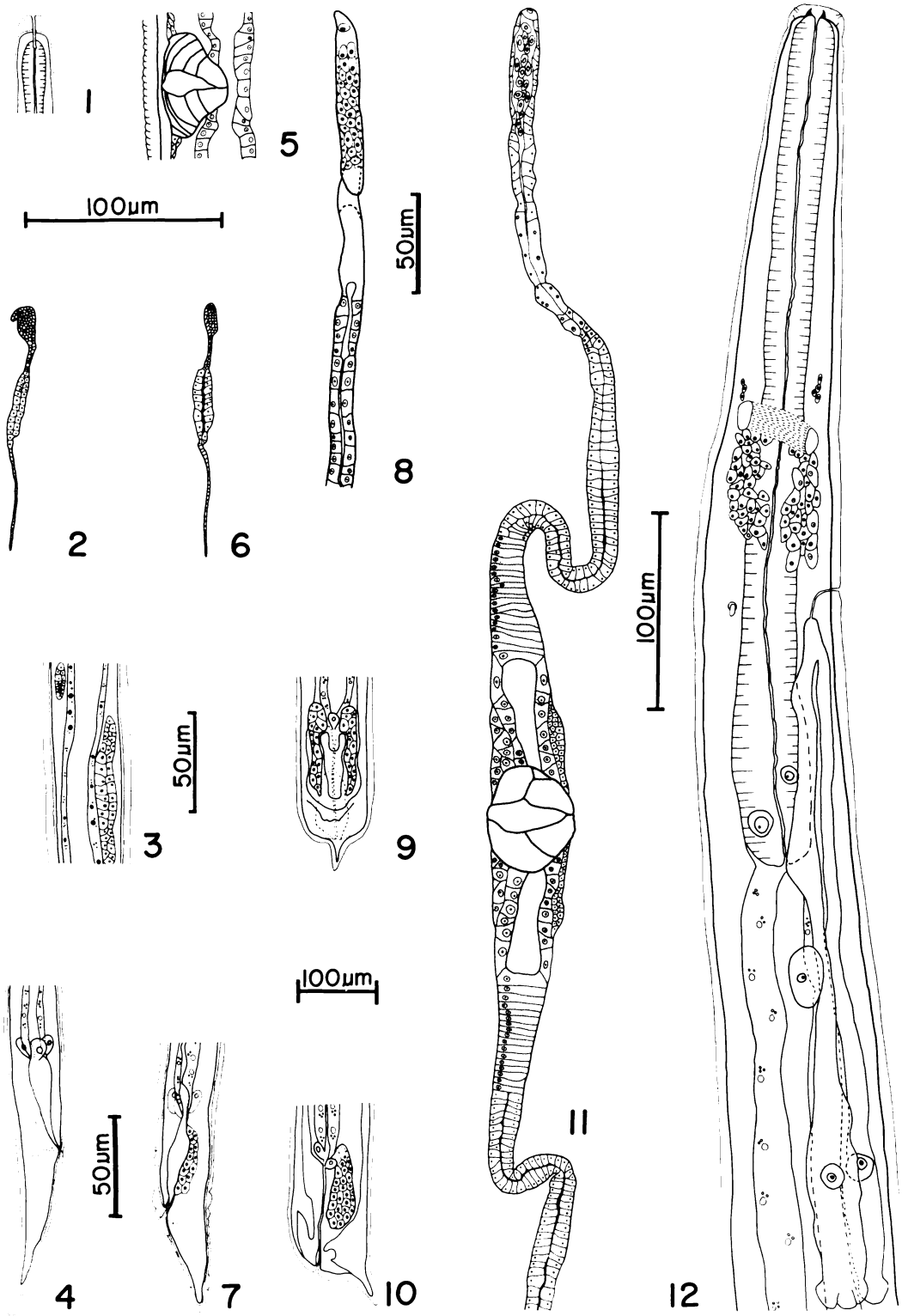
Most worms on day 18 were mature and gravid females were present. However, many adult females were degenerate and some were dead. Males appeared normal and spicules were fully sclerotized.

Few females were present at 22 days. Some females were gravid and others were degenerate. Only three adult males were recovered at 45 days. Petechiae were observed on the stomach mucosa 22 days post-infection.

Adult worms were found in all regions of the stomach of infected rabbits but tended to aggregate in small groups. Immature and mature worms were found lying on the mucosal surface within a layer of mucus. The anterior extremity of immature and mature worms was usually embedded in the mucosa. Occasionally worms were found within ingesta.

Description of stages

Molting third-stage larva (Figs. 1–4, 6–7; Tables 3, 4) (n = 15 males and n = 15 females, 3 days): Buccal capsule still visible during molt (Fig. 1). Genital primordium of male elongate with thin projection of cells extending posteriorly and with broad projection of cells extending anteriorly (Figs. 2, 6). Anterior pro-



jection curving laterally to form terminal hook-like process (Fig. 2). Genital primordium of female in form of broad projection of cells extending anteriorly and posteriorly (Fig. 3). Tail of female long and tapered (Fig. 4). Tail of male slightly swollen distally near anus (Fig. 7).

Fourth-stage larva (Figs. 5, 8–12; Tables 3, 4): *General:* Cuticle thin with fine transverse striations. Lateral alae absent. Circumoral annulus lightly sclerotized. Oral opening circular. Six cephalic papillae and laterodorsal amphids present. Buccal capsule absent. Esophagus filariform with slight swelling near esophageal–intestinal junction. Metacorpus indistinct. Esophageal bulb and valves absent. Esophageal gland nuclei prominent. Nerve ring prominent. Deirids usually at same level, slightly posterior to excretory pore. Excretory system rhabditoid. Lateral excretory canals in region of esophagus prominent. Excretory pore conspicuous. Excretory duct short, lined with thin cuticle. Excretory glands large with salient nuclei. Excretory glands extending posterior to esophageal–intestinal junction, distal extremity often lobed. Three pseudocoelomocytes present, two in region of anterior intestine and one anterior to genital primordium.

Male ($n = 15$, 6 days): Genital primordium well developed, sometimes reflexed at anterior extremity. Germinal zone of testis short, spermatogonia present. Growth zone of testis short, lacking spermatocytes. Vas deferens long, extending to cloaca, with cuboidal epithelial cells, lumen of glands prominent. Bursa incompletely developed. Anus subterminal. Terminal spine present.

Female ($n = 15$, 6 days): Genital primordium didelphic, short. Vulva not patent. Vagina uterina short, proximally consisting of small round or cuboidal cells surrounding a large lumen; distally consisting of large elongate cells. Oviduct long, reflexed, consisting of high columnar epithelial cells. Ovary with short growth zone and short germinal zone. Germinal zone containing oogonia. Tail long and tapered. Phasmids not observed.

Molting fourth-stage larva (Tables 3, 4) ($n = 15$ males and $n = 15$ females, 8–11 days): Excretory gland elongated. Hooks present at distal extremity of weakly developed spicules. Incompletely developed lateral lobes of bursa present. Distal convergence of anteroventral and posteroventral rays apparent. Reproductive tract of female larvae reflexed at extremities. Vulva patent. Phasmids sometimes visible on female larvae.

Immature fifth-stage worms (11–16 days): Longitudinal ridges poorly developed. Number of longitudinal ridges varying in different body regions but remaining relatively constant in each region. Near nerve ring longitudinal cuticular ridges numbering 38 ± 3 (34–41) in males and 55 ± 3 (53–59) in females. At midbody longitudinal cuticular ridges numbering 67 ± 3 (61–71) in males and 102 ± 6 (91–112) in females. Near distal extremity of spicules longitudinal cuticular ridges numbering 44 ± 10 (30–55) in males and 72 ± 3 (68–77) near anus in females. Each spicule with circular lumen and two small, dorsal and ventral alae. Alae at distal extremity of spicules enlarged to form channel between spicules. Distal portion of vas deferens in immature male differentiated into ejaculatory duct with elongate posteriorly-directed cells.

Reproductive tract of immature female fully developed. Eggs absent. Uteri long, slightly expanded laterally with elongate and cuboidal

←

FIGURES 1–12. *Obeliscoides cuniculi multistriatus* Measures and Anderson, 1983. 1. Anterior extremity of molting female third-stage larva, lateral view. Note buccal capsule. 2. Genital primordium of molting male third-stage larva, ventral view. 3. Genital primordium and pseudocoelomocyte of molting female third-stage larva, lateral view. 4. Posterior extremity of molting female third-stage larva, lateral view. 5. Vulva of female fourth-stage larva at 6 days, right lateral view. 6. Genital primordium of molting male third-stage larva, lateral view. 7. Posterior extremity of molting male third-stage larva, lateral view. 8. Distal extremity of reproductive tract of male fourth-stage larva at 6 days, lateral view. Note germinal zone of testis with spermatogonia, growth zone of testis and vas deferens. 9. Posterior extremity of male fourth-stage larvae at 6 days, dorsal view. Note spicule primordia. 10. Posterior extremity of male fourth-stage larva at 6 days, lateral view. Note spicule primordia. 11. Reproductive tract of female fourth-stage larva at 6 days, left lateral view. Note vulva, vagina uterina, reflexed oviduct and ovary with oogonia. 12. Anterior extremity of female fourth-stage larva at 6 days, lateral view. Note large excretory glands, pseudocoelomocyte and circumoral annulus.

TABLE 3. Major dimensions[a] of parasitic stages of male *Obeliscoides c. multistriatus* Measures and Anderson, 1983 from domestic rabbits.

Stage	Molting third stage	Fourth stage	Molting fourth stage	Mature fifth stage	Mature fifth stage
Time of necropsy[b]	3	6	8	16	22
Number	15	15	15	15	15
Length (mm)	1.1 ± 0.1 (0.9–1.2)	3.9 ± 0.4 (3.0–4.6)	4.5 ± 0.1 (4.3–4.7)	9.4 ± 0.4 (8.8–10.4)	9.6 ± 0.4 (9.1–10.4)
Width[c]	30 ± 2 (27–35)	94 ± 12 (81–123)	89 ± 10 (76–114)	127 ± 13 (93–141)	120 ± 6 (107–131)
Nerve ring[d]	117 ± 14 (98–139)	198 ± 16 (166–220)	212 ± 11 (196–233)	281 ± 24 (235–314)	283 ± 14 (255–308)
Excretory pore[d]	147 ± 11 (126–173)	285 ± 23 (249–330)	289 ± 17 (261–321)	429 ± 41 (323–488)	423 ± 26 (395–493)
Deirid[d]	—	296 ± 23 (260–344)	301 ± 17 (272–329)	452 ± 41 (344–508)	463 ± 26 (409–506)
Esophagus length	229 ± 25 (194–284)	410 ± 32 (350–472)	455 ± 22 (411–497)	595 ± 30 (545–649)	599 ± 24 (565–640)
Genital primordium[d]	652 ± 61 (564–769)	—	—	—	—
Genital primordium length	88 ± 20 (51–117)	—	—	—	—
Testis[d]	—	2,800 ± 280 (2,200–3,200)	3,050 ± 101 (2,800–3,200)	2,500 ± 848 (1,100–4,000)	1,390 ± 402 (890–2,200)
Spicule length	—	113 ± 31 (62–197)	331 ± 87 (124–420)	530 ± 22 (490–554)	520 ± 27 (474–587)
Prebursal papillae[e]	—	—	—	448 ± 56 (352–559)	468 ± 20 (441–493)
Tail length	50 ± 11 (36–70)	—	—	—	—

[a] Measurements in micrometers, unless otherwise indicated. Values are mean ± SD (range).
[b] Days post-infection.
[c] At esophageal–intestinal junction.
[d] From anterior extremity.
[e] From posterior extremity.

TABLE 4. Major dimensions[a] of parasitic stages of female *Obeliscoides c. multistriatus* Measures and Anderson, 1983 from domestic rabbits.

Stage	Molting third stage	Fourth stage	Molting fourth stage	Gravid fifth stage
Time of necropsy[b]	3	6	11	18
Number	15	15	15	15
Length (mm)	1.1 ± 0.1 (1.0–1.2)	4.9 ± 0.3 (4.4–5.3)	8.1 ± 0.03 (6.8–8.8)	17.7 ± 1.6 (15.1–19.7)
Width[c]	32 ± 3 (27–36)	106 ± 14 (80–124)	130 ± 16 (109–161)	200 ± 21 (165–256)
Nerve ring[d]	117 ± 13 (87–134)	205 ± 26 (163–249)	261 ± 25 (223–310)	372 ± 48 (278–444)
Excretory pore[d]	144 ± 14 (120–170)	301 ± 42 (233–387)	377 ± 38 (288–435)	579 ± 53 (509–673)
Deirid[d]	—	315 ± 41 (240–397)	396 ± 39 (302–449)	610 ± 54 (497–709)
Esophagus length	230 ± 26 (186–267)	450 ± 54 (376–511)	614 ± 32 (570–686)	837 ± 28 (767–881)
Genital primordium[d]	793 ± 92 (603–922)	—	—	—
Genital primordium length	62 ± 24 (24–116)	—	—	—
Ovary[d]	—	3,500 ± 217 (3,100–3,900)	5,000 ± 639 (4,200–6,400)	2,200 ± 802 (1,200–4,500)
Vulva[d]	—	3,900 ± 234 (3,500–4,100)	6,400 ± 472 (5,200–7,000)	13,500 ± 1,400 (10,700–16,200)
Tail length	63 ± 10 (47–81)	142 ± 21 (104–190)	151 ± 26 (118–200)	259 ± 28 (210–301)
Phasmids[e]	—	—	—	63 ± 16 (40–82)

[a] Measurements in micrometers, unless otherwise indicated. Values are mean ± SD (range).
[b] Days post-infection.
[c] At esophageal–intestinal junction.
[d] From anterior extremity.
[e] From posterior extremity.

cells. Few ootids visible at oviduct–uterus junction. Vagina uterina with large infundibula proximal to each uterus. Two muscular cylindrical sphincters each distal to oval vestibule present. Vagina vera lined with thin cuticle. Vulva transverse, lateral slit with poorly developed lips. Thick walls of sphincters, vestibule and vagina vera with oblique muscles.

Growth was rapid up to 16 to 18 days (Tables 3, 4).

Longevity of infection of *O. c. multistriatus*

The prepatent period in all domestic rabbits was 22 days. Eggs were passed for 81 (61–118) days. At necropsy only adult males (0–40 in number) were recovered in rabbits which had ceased passing eggs.

Host specificity of *O. cuniculi*

Experiment I: Obeliscoides c. multistriatus was recovered from most experimentally infected animals (Table 1). One cottontail rabbit examined 32 days post-infection and two cottontail rabbits examined 25 days post-infection were not infected. These three animals are not included in Table 1. The number of longitudinal cuticular ridges midbody in worms recovered from all experimentally infected hosts was characteristic for *O. c. multistriatus*.

The prepatent period in woodchucks was longer than that in snowshoe hares, cottontail rabbits and domestic rabbits (Table 1). Mature female worms recovered from woodchucks were 16.3 ± 1.2 mm (14.8–18.1 mm, $n = 10$) long and those recovered from snowshoe hares were 19.5 ± 1.0 mm (17.8–20.9 mm, $n = 10$) long. Mature female worms recovered from the domestic rabbit were 20.1 ± 0.8 mm (19.5–21.4 mm, $n = 10$) long and were significantly shorter ($P < 0.05$) than those recovered from woodchucks and snowshoe hares. Mature male and female worms recovered from cottontail rabbits were 10.7 ± 1.0 mm (9.6–12.3 mm, $n = 5$) long and 19.2 ± 1.5 mm (17.3–20.5 mm, $n = 4$) long respectively. Mature male and female worms from the domestic rabbit killed 23 days post-infection were 10.2 ± 0.6 mm (9.8–11.2 mm, $n = 5$) long and 20.4 ± 1.5 mm (18.9–22.3 mm, $n = 5$) long respectively and were not significantly shorter ($P < 0.05$) than those recovered from cottontail rabbits.

Experiment II: All animals were infected with *O. c. cuniculi*. One snowshoe hare which died 5 days post-infection had 19 male fourth-stage larvae, 28 female fourth-stage larvae and two molting third-stage larvae. All remaining snowshoe hares had adult worms when examined. One snowshoe hare, patent and killed 17 days post-infection had 97 worms (47 males, 50 females). The remaining four snowshoe hares were patent 18 days post-infection. These hares had 98 (52 males, 46 females), 88 (22 males, 66 females), 24 (6 males, 18 females) and 86 (48 males, 38 females) worms when examined 22 days post-infection. Lesions were not observed in infected animals. The domestic rabbit was patent 18 days post-infection. The number of longitudinal cuticular ridges midbody in worms recovered from all experimentally infected animals was characteristic of *O. c. cuniculi*.

Experiment III: a) Domestic rabbits—One fourth-stage larva and 33 immature worms were found in one rabbit 18 days post-inoculation and two adult worms were recovered from the other control rabbit at 32 days.

b) Swiss Webster mice—Six third-stage larvae were found at 2 days. One third-stage larva was found at 7 days. No worms were found at 17 days.

c) Wistar rats—One third-stage larva was recovered at 2 days. No worms were found at 5 and 17 days.

d) Syrian hamsters—Six third-stage larvae were recovered at 2 days. Twelve fourth-stage larvae were found at 7 days and one fourth-stage larva at 17 days.

e) Guinea pigs—Worms were not found in one guinea pig killed at 2 days. One third-stage larva was found at 5 days. Six fourth-stage larvae were found at 14 days.

f) Gerbils—Third-stage larvae were recovered from gerbils in the first 6 days post-inoculation. Fifty-seven, five, 20 and one larvae were recovered 2, 2, 4 and 6 days post-inoculation. Fourth-stage larvae were recovered from gerbils 7 to 21 days post-inoculation. The greatest number of larvae recovered was 47 at 7 days post-inoculation. This gerbil had been given 200 infective larvae. Only one to four larvae were recovered at 8, 10, 14, 18 and 21 days post-inoculation. Larvae were all early fourth-stage.

DISCUSSION

Third-stage larvae exsheathed within 24 hr in domestic rabbits and were found within the

mucosa. Sollod et al. (1968) observed exsheathed third-stage larvae in ingesta 1 hr post-inoculation and in the mucosa 24 hr post-inoculation. In the present study, the third molt occurred 3 days post-inoculation and male and female worms were distinguished at this time.

Sollod et al. (1968) found fourth-stage larvae in rabbits 5 days post-infection. They also observed molting fourth-stage or early fifth-stage worms 10 days post-infection. Fifty-eight percent of worms recovered 14 days post-infection were fifth stage of which the majority were on the surface of the mucosa (Sollod et al., 1968).

Alicata (1932) noted that development of *O. cuniculi* in guinea pigs was similar to that in domestic rabbits. However, worms first molted 2 days post-infection in guinea pigs. Males molted the second time 7 days post-infection. Adult males and molting fourth-stage females were recovered 12 days post-infection. He observed gravid females in guinea pigs 17 days post-infection.

In the present study, females were gravid 18 days post-infection and the prepatent period in rabbits was 16–22 days. Alicata (1932) reported that the prepatent period in rabbits was 16 to 20 days. Sollod et al. (1968) noted that the prepatent period in two rabbits was 19 and 25 days. Worley (1963) reported a prepatent period of 16 to 23 days with an average of 19 days in rabbits.

Growth of parasitic stages was rapid in the present study. Some structures such as intestine, spicules and reproductive tract increased in length proportionately as worms grew. Tail length and esophagus length decreased proportionately as worms grew. Length and growth rate of male and female worms were similar until 16 days when both were sexually mature. At this time females continued to increase in length while males did not. Sollod et al. (1968) observed a similar difference in growth after worms were sexually mature.

Lesions other than petechiae were not seen in experimentally infected rabbits. Alicata (1932) observed lesions in experimentally infected rabbits but not guinea pigs. Sollod et al. (1968) found petechiae and thick mucus on the stomach mucosa in experimentally infected rabbits five days post-infection. Worley (1963) and Russell et al. (1966) also noted petechiae in experimentally infected rabbits. MacLulich (1937) reported a yellowish, thick fluid in the stomach of six snowshoe hares infected with large numbers of *O. cuniculi* in Ontario. Erickson (1944) observed petechiae and a thickened stomach mucosa in the pyloric area of snowshoe hares infected with *O. cuniculi* in Minnesota. Gastric erosion was noted in some cottontail rabbits infected with *O. cuniculi* in Virginia (Jacobson et al., 1978).

The synlophe was not visible in fourth-stage larvae and was incompletely developed in the early fifth stage. Ridges were poorly developed 14 days post-inoculation. Lee (1970), in an ultrastructural study of the cuticle of *Nippostrongylus brasiliensis*, observed that longitudinal cuticular ridges were not fully formed in early molting fourth-stage larvae. Durette-Desset (1971) observed that the synlophe of some trichostrongyloids was poorly developed in fourth-stage larvae compared to that in adults.

Spermatozoa were observed in the reproductive tract of males and also in the proximal part of uteri of females 16 days post-inoculation. Copulation probably occurs 15 to 16 days post-inoculation since spermatozoa were not observed in males 14 days post-inoculation.

Alicata (1932) found mature males and degenerate females 161 days post-infection in a domestic rabbit given an undetermined number of larvae of *O. cuniculi*. Worley (1963) reported an average patent period of 138 days and two rabbits given many larvae were patent for more than 196 days. Russell et al. (1966) found that the number of arrested fourth-stage larvae of *O. cuniculi* varied directly with the number of larvae inoculated. As some worms ceased producing eggs and died, they were apparently replaced by worms which had been arrested. This would influence the length of the patent infection. In the present study, the number of larvae inoculated was small and infections were of short duration. A few adult males were recovered after females had disappeared.

Alicata (1932) successfully infected guinea pigs with *O. cuniculi* but fewer worms matured in guinea pigs than in rabbits. Worley (1963) induced in immature guinea pigs transient infections of *O. cuniculi* originally obtained from a wild infected cottontail rabbit. He was unable to infect young mice, rats and hamsters. In the present study, transient infections of *O. c. multistriatus* were produced in mice and rats. *Obeliscoides c. multistriatus* developed to the fourth stage in hamsters and guinea pigs. Ger-

bils did not develop patent infections. Thus, these small rodents appear to be unsuitable hosts for *O. c. multistriatus*.

In addition to domestic rabbits, patent infections of *O. c. multistriatus* developed in snowshoe hares, cottontail rabbits and woodchucks. Fewer *O. c. multistriatus* were recovered from cottontail rabbits than snowshoe hare, woodchucks and domestic rabbits and three cottontail rabbits did not become infected. However, snowshoe hares given *O. c. cuniculi* developed patent infections. Thus, cottontail rabbits appear less susceptible to infection with *O. c. multistriatus* and this may relate to the recent subspeciation of this nematode (Measures and Anderson, 1983a).

ACKNOWLEDGMENTS

We extend our appreciation to Dr. David Worley of Montana State University for providing infective larvae of *O. c. cuniculi* and to C. Bartlett for kindly supplying snowshoe hares and cottontail rabbits. We wish to thank staff of the Central Animal Facility, University of Guelph for care of experimental animals and assistance provided to the authors during this study. The advice and assistance of U. Strelive in preparation of drawings is greatly appreciated. This work was funded through a grant from the National Science and Engineering Research Council of Canada.

LITERATURE CITED

ALICATA, J. E. 1932. Life history of the rabbit stomach worm, *Obeliscoides cuniculi*. J. Agric. Res. (Washington, D.C.) 44: 401–419.

DURETTE-DESSET, M.-C. 1971. Essai de classification des nématodes Heligmosomes. Corrélations avec la paléobiogéographie des hôtes. Mem. Mus. Natl. Hist. Nat. Série A, Zoologie. Tome LXIX, 126 pp.

ERICKSON, A. B. 1944. Helminth infections in relation to population fluctuations in snowshoe hares. J. Wildl. Manage. 8: 134–153.

JACOBSON, H. A., R. L. KIRKPATRICK, AND B. S. MCGINNES. 1978. Disease and physiologic characteristics of two cottontail populations in Virginia. Wildl. Monogr. 60, 53 pp.

LEE, D. L. 1970. Molting in nematodes: The formation of the adult cuticle during the final molt of *Nippostrongylus brasiliensis*. Tissue Cell 2: 139–153.

MACLULICH, D. A. 1937. Fluctuations in the numbers of the varying hare (*Lepus americanus*). Univ. Tor. Studies, Biol. Series No. 43, 136 pp.

MEASURES, L. N., AND R. C. ANDERSON. 1983a. New subspecies of the stomach worm, *Obeliscoides cuniculi* (Graybill), of lagomorphs. Proc. Helminthol. Soc. Wash. 50:1–14.

———, AND ———. 1983b. Development of free-living stages of *Obeliscoides cuniculi multistriatus* Measures and Anderson, 1983. Proc. Helminthol. Soc. Wash. 50:15–24.

RUSSELL, S. W., N. F. BAKER, AND G. S. RAIZES. 1966. Experimental *Obeliscoides cuniculi* infections in rabbits: Comparison with *Trichostrongylus* and *Ostertagia* infections in cattle and sheep. Exp. Parasitol. 19: 163–173.

SOLLOD, A. E., T. J. HAYES, AND E. J. L. SOULSBY. 1968. Parasitic development of *Obeliscoides cuniculi* in rabbits. J. Parasitol. 54: 129–132.

WALLACE, F. G. 1942. The stomachworm, *Obeliscoides cuniculi* in the woodchuck. J. Wildl. Manage. 6: 92.

WORLEY, D. E. 1963. Experimental studies on *Obeliscoides cuniculi*, a trichostrongylid stomach worm of rabbits. I. Host-parasite relationships and maintenance in laboratory rabbits. J. Parasitol. 49: 46–50.