

Review of Life Cycles of Some Parasitic Nematodes in Mammals in Research Associated with the University of Kentucky

E.T. Lyons, Veterinary Science

Abstract

This review is on research associated with the University of Kentucky (UK) on life cycles of some parasitic nematodes in mammals. It includes the first report of a larval helminth (acanthocephalan, cestode, nematode, or trematode) transmitted through the mammary system of a female mammal to her offspring in which it develops to the adult stage. The parasite is a nematode, the intestinal hookworm (*Uncinaria lucasi*) in northern fur seals (*Callorhinus ursinus*). After discovery of transmammary transmission of hookworms in fur seals, the first finding of this manner of infection was found for an intestinal nematode in the genus *Strongyloides* in equids, bovids and ovids. Later, transmammary transmission of the hookworm *Uncinaria* spp. was found for the first time in California sea lions (*Zalophus californianus*). Thus in research associated with UK, definite transmammary transmission of nematodes was found for the first time in five different host species. In addition, highly probable transmammary transmission of *Uncinaria lucasi* first was found for a sixth host, Steller sea lions (*Eumetopias jubata*). Another aspect of research resulted in the first experimental completion of the life cycle of the eyeworm *Thelazia lacrymalis*: larval stages in face flies (*Musca autumnalis*) and the adult stage in equids.

Introduction

Most internal parasites of vertebrates require stages outside the host for development and transmission. Some life cycles are simple and straightforward. Others may have one or more intermediate or paritonic hosts. Knowledge of life cycles of parasites first of all is of great scientific interest. Secondly, life cycles are of great importance in controlling parasites.

The object of this presentation is to review life cycles of some mammalian parasitic nematode species in research in association with the University of Kentucky.

Transmammary Transmission

Hookworms

Northern fur seals (*Callorhinus ursinus*)

The majority of the review in this paper will be on studies on hookworms in northern fur seals (NFS) (*Callorhinus ursinus*). This is because most of the research reported here is on determination of the life cycle of these parasites in this pinniped host and the solving of the manner of infection of the pups. Thus, justification for emphasis on the life cycle of these hookworms was the discovery of a previously unreported method of helminth parasite transmission in mammals and the far-reaching importance of the finding.

O.W. Olsen, from Colorado State University, started doing research on hookworms in NFS on St. Paul Island (SPI), Alaska in 1951 and he published his research findings through 1958. The reason for this research was that *U. lucasi* were the cause of ill health and even death of pups. In effect, his main objective was to find a way or ways to control the hookworms to alleviate the health problem these parasites were causing in pups.

Olsen learned many aspects of hookworm disease, some of which included: (1) the pathologic condition in pups; (2) intestinal infection of pups was at a very young age—even when born on rocks near the ocean; (3) free-living third stage larvae (FL₃) would not mature in pups; (4) adult hookworms were not found in NFS older than pups; (5) only one stage of hookworms was found at a time in the intestines of pups; (6) FL₃ experimentally placed on various body areas of pups penetrated the flipper skin more readily; and (7) cresylic acid (5 percent) sprayed on rookery soil before the breeding season killed FL₃, but this did not result in a decline of deaths, prevalence, and number of hookworms in pups. The most noteworthy facet of the research by Olsen through 1958 was that the life

Table 1. First discovery of transmammary transmission of nematodes in research associated with the University of Kentucky.

	Parasite	Host	Geographical Location
Definite	Hookworms <i>Uncinaria lucasi</i>	Northern fur seals <i>Callorhinus ursinus</i>	Alaska
	Intestinal threadworms <i>Strongyloides westeri</i>	Equids <i>Equus caballus</i>	Kentucky
	Intestinal threadworms <i>Strongyloides papillosus</i>	Bovids <i>Bos taurus</i>	
		Ovids <i>Ovis aries</i>	
	Hookworms <i>Uncinaria</i> spp.	California sea lions <i>Zalophus californianus</i>	California
Probable	Hookworms <i>Uncinaria lucasi</i>	Steller sea lions <i>Eumetopias jubata</i>	Alaska

cycle of hookworms in the pups was not typical for hookworms and many other species of nematodes in other hosts. Most unusual was that FL₃ would not mature in pups in experimental attempts.

Over a total of 13 months in 1960, 1961, and 1962, the present author, who had worked at UK from 1958-1960 and came back in 1963, did research on hookworms in fur seals on SPI as a graduate student of O.W. Olsen with whom he worked closely. The major goal was to concentrate on exactly how pups became infected with hookworms which mature in the gut of pups. This part of the life cycle had evaded discovery since the late 1800s when hookworms first were found in fur seals on SPI.

Major interest on research in 1960 was to try and determine if the source of hookworms which mature in pups was from larvae acquired prenatally. The premise for this approach was that Olsen had observed that the mother seemed to play a role in infection of her pup. One basis for this was that, as mentioned previously, young pups born by the ocean on rocks washed by the tide going in and out, developed patent infections. Also killing FL₃ on the ground by cresylic acid did not decrease infections in the pup. Thus, there were indications that the mother might be the culprit. Tissues from all parts of the body of fetuses, still-borns, and recently deceased new-born pups were examined and found negative

for hookworms. Pups taken by Caesarian section were held in captivity for at least two weeks, the prepatent period for hookworm natural infections; none became infected. Therefore, based on a fairly small sample size, there was no evidence of prenatal infection. At least some of these pups should have been positive for hookworm larvae if prenatal infection did indeed occur because the prevalence of natural infections of mature hookworms in pups was almost 100 percent on several rookeries in the 1960s.

Exactly how the pups became infected was a great mystery. It appeared that there must be an atypical and highly unusual form of hookworm transmission. It was known that the pups were positive for hookworms very soon after birth. Even though no evidence of prenatal infection was found, it still seemed that the mother was involved somehow in infecting her pup. Therefore, in 1961, an experiment was designed to try and learn if pups were infected by involvement of: (1) the mother only, (2) the mother plus rookery, and/or (3) a specific time period postpartum. Thirty pregnant cows were captured, assigned to separate groups (10/group), and placed in individual cages. The protocol was: **Group 1**—put on rookery soil and, on each of days one to five postpartum, take two pups to “clean ground” (area never inhabited by fur seals and thus no hookworm FL₃ present in soil or vegetation) for one day

and then return them to their mothers; **Group 2**—put on “clean ground” and on each of days one to five postpartum, take two pups to rookery soil for one day and then return them to their mothers; **Group 3**—put on “clean ground” as controls and leave the pups with their mothers. This study resulted in solving how pups are infected with hookworms; this breakthrough happened on July 4, 1961.

Some highlights of the 30 pregnant-cow-study: (1) nine of ten control pups (Group 3) were positive for gastrointestinal infections of hookworms and (2) young pups, one of them only two hours old, harbored hookworm larvae in milk in their stomachs. Other findings: (1) parasitic L₃ hookworms were recovered from a mixture of mammary tissue, ventral abdominal blubber, and milk from dead pregnant cows; (2) when parasitic L₃ from the preceding source were administered by stomach tube to Caesarean pups, intestinal infections developed; the prepatent period was about two weeks; (3) parasitic L₃ (1-135/cow) were recovered from milk samples of seven of eight pregnant cows; (4) parasitic L₃ also were recovered from ventral abdominal tissues (VAT) of fur seal nonpregnant cows, bulls, bachelors, two-

Life cycle of *Uncinaria lucasi* in northern fur seals

A brief summary (Figures 1a, 1b).

Pups

- Parasitic L₃ are ingested in the “first milk” of the mother and mature in about two weeks; adult female hookworms lay eggs which are passed in the feces.
- Adult hookworms are spontaneously lost after two to three months.

Rookery soil

- Free-living L₃ hatch from eggs in late summer and enter seal tissues after oral/percutaneous infection.

Fur seals—all ages/both sexes

- Parasitic L₃ are found in tissues, predominantly the ventral abdominal blubber.
- Parasitic L₃ are at a “dead end” in tissues except for parturient cows.

Parturient cows

- Parasitic L₃ pass in the “first milk” to their pups for a very short time postpartum; they are the only stage which matures in pups.
- Parasitic L₃ in tissues live and are infective for several years.

year-old males, yearlings, and pups, and from Steller sea lion subadults. However, parasitic L₃ from these sources, contrary to those from VAT of pregnant cows, did not mature or undergo any development in the gut of experimentally exposed Caesarean NFS pups.

The life cycle finally was deciphered, showing that the source of infections of adult hookworms in pups is from parasitic L₃ passed in the first milk of

their mothers. This was the first report of a larval helminth (acanthocephalan, cestode, nematode, or trematode) transmitted through the mammary system of a female mammal to her offspring in which it develops to the adult stage. Numerous other facets of the life cycle were learned from the research in the early 1960s and in later research on hookworms in northern fur seals but will not be mentioned here.



Figure 1a. Cow in center nursing newborn pup with placenta still attached.

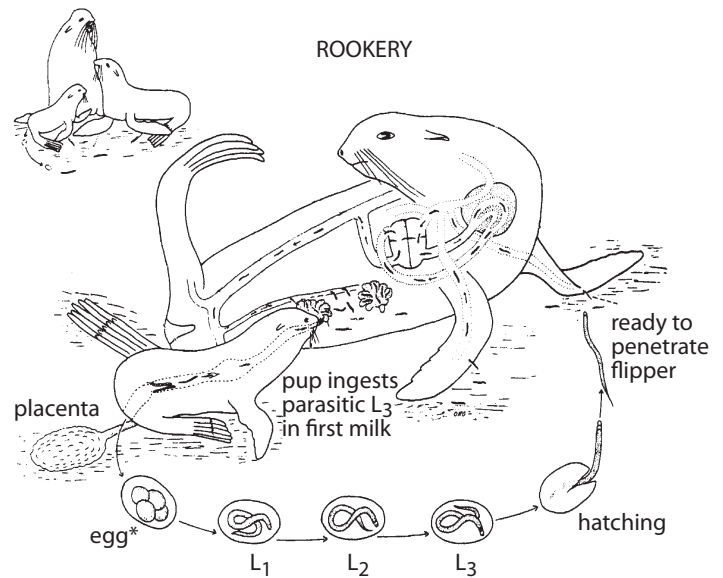


Figure 1b. Free-living hookworm stages (eggs/larvae) on rookery. Adapted from drawing by O.W. Olsen.



Figure 2.

Life cycle of *Strongyloides westeri* in equids

A brief summary (Figure 2).

Foals

- Parasitic L₃ in the milk of dams are probably the major source of infective larvae maturing in foals.
- Free-living L₃ can infect foals orally and/or percutaneously and mature but are probably a minor source of maturation in foals; they also can migrate to tissues
- Adult *S. westeri* lay eggs first passed in feces at about two weeks of age; these adults are spontaneously eliminated when the foal is a few months of age.

Mares

- Parasitic L₃ are passed to foals in milk beginning a few days postpartum and continuing for several weeks
- Parasitic L₃ are stored in tissues and only mobilized during early lactation.

Steller sea lions (*Eumetopias jubata*)

There was no opportunity to examine milk from the Steller sea lions. However, there is a strong indication that transmammary transmission of *U. lucasi* does occur. This observation is based on: (1) specimens of *U. lucasi* from this host have the same molecular make-up as do specimens from northern fur seals; (2) measurements of adult *U. lucasi* are larger than specimens from NFS pups but are just considered larger because of being in a bigger host; (3) parasitic L₃ hookworms have been recovered in plentiful numbers from ventral abdominal blubber of this host. Thus, in all probability, hookworms do infect Steller sea lion pups through the mammary system of their mother. This phenomenon needs to be verified by examination of the first milk of cows.

California sea lions (*Zalophus californianus*)

Parts of several studies showed that *Uncinaria* spp. (species uncertain) are transmitted to pups through the milk of their mother. Parasitic L₃ were found in the milk of two cows and in milk in the stomach of one newborn pup and one pup about two days old. Also, these larvae have been found in large numbers in ventral abdominal blubber and adjoining tissues of several cows.

Intestinal threadworms

Equids (*Equus caballus*)

Prior to extensive research on the life cycle of *S. westeri* in equids, several aspects were known in 1963. Some of them included: (1) prevalence in the Central Kentucky area was about 90 percent in foals; (2) most infected foals were passing eggs in their feces at about two weeks of age; (3) foals were infected regardless of the time of the year or place of birth; (4) indications were that foals were infected at or very soon after birth; (5) intestinal infections were eliminated spontaneously at a few months of age; and (6) older equids usually do not have adult enteric infections.

In an attempt to understand the life cycle better, foals (n = 158) were removed from their dams at 0 to 11 days of age and raised in cages. Only eight of these foals became positive for eggs in their feces; two of them were less than four days old when taken from their dams. These findings contradicted the theory of early infection, but they substantiated indications that prenatal infection did not occur.

Next, worm-free foals (n = 10) experimentally were exposed to free-living L₃ *S. westeri* and all began passing eggs at 10-14 days later. The prepatent period was similar to the age when naturally

infected foals first began passing eggs. This was more indication that foals are naturally infected at an early age.

A study was designed where pregnant mares (n = 7) were put in separate isolated areas with no strongyloides free-living L₃ present. Foals born to six of the seven foals began passing eggs at about 14 days of age. These results showed that there was a strong indication that the dam was involved in infecting her foal. Examination of mare tissue, excretions/secretions, including colostrum, resulted in no *S. westeri* larvae being recovered. Also, tissues of fetuses and newborn foals were negative for *S. westeri* larvae, providing further suggestion of absence of prenatal infection.

Thus, the source of the primary infection in foals was puzzling. It definitely was proven that foals were infected soon after birth. The question was: "What could be the main source of infection if not prenatal, colostrum, or environmental?" The answer to this was found when a foal was removed from its dam at birth, placed in a cage where an environmental source of larvae was not possible, its dam milked five times a day for 20 days and a portion of colostrum/milk was examined for larvae; the remainder was fed to her foal. One larva was found in milk at 11 days postpartum and the foal was passing eggs at 15 days of age.

At 20 days of age, the foal was euthanized and eight adult *S. westeri* were found in its intestines. Subsequently, milk was collected from 82 mares and 32 were passing parasitic L₃ at 4 to 47 days postpartum. Usually, a low number of larvae were found in the milk samples. Larvae were found in the mammary glands of two mares at necropsy. Parasitic L₃ from milk of mares were administered via stomach tube to seven worm-free foals. Eggs were found in the feces of six foals at eight or nine days later and at 12 days for the seventh foal. The latter study demonstrated that parasitic L₃ in the milk were capable of maturing in foals. As sometimes happens in research, the “missing link” in the *S. westeri* life cycle was that larvae were not in the colostrum like with *U. lucasi* but first passed in milk a few days postpartum and continued doing so for several days. Several other aspects of the life cycle have been learned but not reported here.

Ovids (*Ovis aries*)

Bovids (*Bos taurus*)

Various aspects of the life cycle of these parasites had been studied in sheep and cattle by many researchers but not the possibility of transmammary transmission. Here at UK, *S. papillosus* parasitic L₃ were recovered from the milk of six ewes. The number of larvae ranged from one to four per milk sample but, in the aggregate, ranged from 1 to 21; positive milk samples were between 8 and 19 days postpartum. Colostral samples from three of the ewes were examined and were negative for larvae. One ewe was placed in a cage at two days before lambing; colostrum was negative. Her lamb first passed eggs at 21 days of age.

Milk samples examined on the 8th and 9th day prepartum from a cow were negative. Larvae were detected in milk of the cow on the 7th and 19th days postpartum. One larva was found in each milk sample. *Strongyloides* eggs were first found in the feces of her calf at 15 days after birth.

This study showed that transmammary transmission of *S. papillosus* occurs in sheep and cattle.

Face Fly Transmission

Eyeworms

Equids (*Equus caballus*)

Chitwood and Stoffolano reported the first finding in North America of *Thelazia* spp. larvae in the face fly (*Musca autumnalis*). Early reports of *Thelazia lacrymalis* in horses in North America (NA) were by Barker in Canada and Walker and Beckland in the United States. These reports of finding thelazids in face flies and horses in NA, stimulated interest here at the University of Kentucky to try and ascertain whether face flies are an intermediate host for *T. lacrymalis* and, if so, try to experimentally infect equids. Forty-three laboratory-raised face flies, exposed to *T. lacrymalis* embryos (first-stage larvae) from female worms and killed 1 to 26 days later, were infected with various sizes of larvae. Some of them were L₃. In a later study, face flies were killed at 10 days after exposure to *T. lacrymalis* embryos to collect L₃ in an effort to try to complete the life cycle in worm-free ponies (Figure 3). These larvae were deposited on the conjunctiva at the medial canthus of the eyes of 21 ponies. The ponies were killed at 12 to 106 days post-exposure and *T. lacrymalis* were recovered from the eyes of 17 of the ponies. Results of this first completion of the life cycle from “start to finish” of *T. lacrymalis* established that: (1) face flies (*M. autumnalis*) are an intermediate host for this eyeworm species and (2) sexual maturity of these parasites, defined by active embryos in utero of female worms, was between 67 and 77 days after exposure to L₃.

Remarks

After the transmammary transmission of hookworms in northern fur seals was discovered, this manner of transmission was found to occur for many species of internal parasites in several host species including other pinnipeds: Juan Fernandez fur seals, New Zealand sea lions, and South American sea lions.



Figure 3. Face flies (*Musca autumnalis*) ingesting embryos (first-stage larvae) of the eyeworm, *Thelazia lacrymalis*, in a groove on a glass slide. Development to the third-stage larvae (L₃) occurred in the flies; these L₃ were transferred to eyes of worm-free ponies, in which they developed to adult eyeworms.

It should be mentioned that after the 1960s studies were finished, two references were found in the literature of nematode larvae found in milk: natural infection of *Trichinella spiralis* in human milk and experimental infection of *Ancylostoma caninum* and *Toxocara canis* in guinea pigs. Potential significance of this research was not recognized.

The mechanism of transmammary transmission of nematodes is poorly understood. There is variability in life cycles of parasites with this manner of transmission. Some host species have colostrum transmission, e.g. *Uncinaria lucasi*, *Ancylostoma caninum* in dogs, and *Strongyloides ransomi* in pigs, and others have post-colostral transmission, e.g. *Strongyloides westeri* in horses and *Strongyloides papillosus* in sheep and cattle.

There is at least one similar characteristic of larvae of *U. lucasi* and *S. westeri*. Parasitic third-stage larvae passing through the mammary system of females to their offspring are larger than the free-living third stage. Thus, hormones or some other factor(s): (1) not only cause increased growth of the parasitic L₃ and/or (2) also stimulate movement of them to pass through the mammary system of the mothers after parturition to their young.

One highly unusual aspect of the life cycle of *U. lucasi* in NFS is that the parasitic L₃ is the only stage which matures in pups. The free-living L₃, unlike the typical pattern with other nematodes, does not mature in the intestine but goes to tissues. Transmammary transmission, only with *U. lucasi*, has resulted in a great decrease in prevalence in NFS pups on SPI because the numbers of NFS have declined. Propagation of these nematodes is density related and, if not enough are "recycled," then prevalence is greatly reduced. DeLong has suggested that MHC may be a factor in decreased hookworm prevalence in fur seals on SPI. The preva-

lence of *U. lucasi* is now very low in NFS on SPI, but it remains high in NFS, and the hookworms are devastating, on some rookeries in other geographical areas like San Miguel Island, Calif., and some of the Russian islands.

Significance of the discovery of transmammary transmission of hookworms in northern fur seals was described best by colleagues. The American Society of Parasitologists Newsletter (Volume 18, No.4, December 1996) has a section of Pioneer Papers. In that issue, there is a write-up by Stewart, who did early research on prenatal and transmammary infections of *S. ransomi* in pigs, and Shoop, who was involved on vertical

transmission of helminths. They mention in the Newsletter that in the 100th issue of Parasitology Today milestones in parasitology are cited, mostly related to important life cycles in human infection. Further they state that "However we should recognize an event in veterinary parasitology that revolutionized our concept of many important life cycles." They say that the milestone is the Olsen and Lyons paper describing a new route of transmission of helminths in fur seals. Also Stewart and Shoop mention that, since then, a number of publications have shown milk-borne transmission of several helminths in their life cycles.

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