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REVIEW

Review of research on hookworms (*Uncinaria lucasi* Stiles, 1901) in northern fur seals (*Callorhinus ursinus* Linnaeus, 1758)

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Abstract The objective of this article is to review knowledge on the hookworm *Uncinaria lucasi* Stiles, 1901 in northern fur seals, *Callorhinus ursinus* Linnaeus, 1758. Emphasis is placed on research on this host–parasite system in the Pribilof Islands, AK, USA where the bulk of the studies has been performed.

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Northern fur seals

Classification and geographical location

Northern fur seals (NFS) belong to the family, Otariidae of the pinniped carnivores. They were discovered by G.W. Steller on the Commander Islands in 1741–1742 and by Gerasim Pribilof on St. George Island in 1786; the next year they were detected on St. Paul Island (SPI) (Reeves et al. 1992). These two islands and three much smaller islands in the same group are named the Pribilof Islands, Alaska after their discoverer.

Currently, NFS breed on the Pribilof Islands and Bogoslof Island in the eastern Bering Sea, the Commander Islands in the western Bering Sea, the Kurile Islands in the western North Pacific, Robben Island in the western Okhotsk Sea, and Southeast Farallon, and San Miguel Islands off California in the eastern Pacific (DeLong 2007).

Population on Pribilof Islands and on San Miguel Island

Since their initial discovery on the Pribilof Islands, the population sizes of northern fur seals have fluctuated greatly there because of exploitation and other possible causes. In addition, there has been a precipitous unexplained population decline in the last several decades. Melin et al. (2006) reported that the number of pups on SPI have decreased from about 300,000 to 400,000 in the 1950s and early 1960s to about 120,000 in the early 2000s. Based on research from 2008

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(Ream 2008), the number of pups born has decreased at an annual rate of 5.2% (SE=0.40) since 1998, which is at the level last observed in about 1916.

Northern fur seals were first sighted in 1968 on San Miguel Island, CA where a small colony (about 100) was found (Peterson et al. 1968). The population has increased over the past few decades and now numbers 8,000 to 10,000 fur seals (DeLong et al. 2009). The production of pups has been about 2,500 per year, but approximately half died within 2 months following birth in most recent years.

Breeding cycle on Pribilof Islands

Some attributes of *Callorhinus ursinus* according to Reeves et al. (1992) follow. Sexual size dimorphism is striking with adult males being about five times larger than females.

Females mature at about 4 years of age and males at about 4 to 5 years of age. Adult males (bulls) usually do not breed until 8 or 9 years old; typically, they do not breed for more than about 2 years. There is a territorial reproductive social system on breeding rookeries. A bull may defend, from other bulls, an area large enough to contain a group of 40 or more adult females. Pups are born and nursed in the territory, and females are bred there. Longevity in females of greater than 20 years has been reported but males typically don't live that long.

The basic reproductive cycle of northern fur seals on the Pribilof Islands is as follows: Adult males begin to arrive in May and establish territories. In mid-June, pregnant females (cows) start arriving and continue doing so through July and early August. They usually give birth to a single pup within 1 day after arrival and bond with and nurse their pup for about a week. Females enter estrus and are bred at about 5 to 6 days following parturition. After this first week of nursing their pup, they go to sea and feed for 4 to 6 days, after which they return and nurse their pup for another 2 days. Then, they go back to sea and feed again. This cycle repeats for about 4 months (Gentry and Holt 1987) at which time the pups are weaned and leave the rookery. The pups remain at sea, and a small portion return the next autumn as yearlings, but the majority do not return until they are 3 years old. Therefore, the first pelagic trip for the pups span 10 to 30 months depending upon whether they first return as yearlings, 2-year-olds or 3-year-olds. Nearly all of the bulls and females have left the island by November or early December with males spending the winter in the Bering Sea or North Pacific and females in the North Pacific. Knowledge of the breeding habits and other aspects of fur seal life history is imperative in discovering and understanding facets of the biology of their hookworms.

Hookworms

Classification and pinniped hosts

Lucas (1899) first found hookworms in the small intestine of NFS pups in 1896. He recognized that these nematodes were in the genus *Uncinaria*. Stiles and Hassall (1899) partially described them. Stiles (1901) published a more comprehensive description and named them *Uncinaria lucasi* in honor of Lucas. The genus *Uncinaria* derives from the Latin word *uncus*, meaning hook or barb. Possible reasons for the term hookworm are: (1) the anterior end is in a bent or hooked dorsal position and (2) the hooked feature of the bursal rays at the posterior end of males (Noble and Noble 1964). Photographs of some of these and other features of the morphology of *U. lucasi* from *C. ursinus* and Steller sea lions (*Eumetopias jubata*) have been published (Lyons 2005; Lyons and DeLong 2005).

To date, only two species of pinniped hookworms, *U. lucasi* Stiles 1901 and *Uncinaria hamiltoni* (Baylis 1933, 1947) have been described based on morphological and morphometric characteristics. However, there are reports of specimens that do not fit the descriptions of either *U. lucasi* or *U. hamiltoni* (Baylis 1947; Dailey and Hill 1970; Castinel 2006).

Nadler et al. (2000) showed morphologic and molecular differences between hookworms in NFS and California sea lion (*Zalophus californianus*) pups on San Miguel Island, CA. Recently, Nadler et al. (2009) reported, based on nucleotide sequence data, that hookworms examined from a total of nine pinniped host species included seven different evolutionary lineages. Further investigations are necessary to determine how many different species of hookworms are present among pinniped host species. Hookworms have been reported in otariids (five species of fur seals and five species of sea lions) and in phocids (two species of elephant seals and the ringed seal) (Table 1).

Observations by Lucas (1899)

Lucas, in his investigation of fur seal pup mortality in 1896, thought the major cause of death of pups was from being trampled by bulls. However, in a subsequent investigation in 1897, he decided that hookworms (*Uncinaria* spp.) were the main cause of death in young pups by sucking their blood that resulted in anemia and death. He stated that this is an "infantile disease," and those which do not die before the middle of August "outgrow it."

Research in northern fur seals on the Pribilof Islands in the 1950s

Olsen (1952, 1953, 1954, 1956, 1958, 1959) and Dixon (1955) began a multiyear investigation in 1951 on hook-

Table 1 Pinniped hosts for which hookworms (*Uncinaria* spp.) have been reported

Name	Locality	Selected references
Australian fur seal (*Arctocephalus pusillus*)	Australia	Beveridge (1980)
Juan Fernandez fur seal (*Arctocephalus philippi*)	Chili	Sepulveda (1998)
New Zealand fur seal (*Arctocephalus forsteri*)	Australia	Beveridge (1980)
Northern fur seal (*Callorhinus ursinus*)	USA	Lucas (1899)
South American fur seal (*Arctocephalus australis*)	Uruguay	George-Nacimento et al. (1992)
Australian sea lion (*Neophoca cinerea*)	Australia	Beveridge (1980)
California sea lion (*Zalophus californianus*)	USA	Dailey and Hill (1970)
New Zealand sea lion (*Phocarctos hookeri*)	New Zealand	Castinel (2006)
South American sea lion (*Otaria flavescens*)	Argentina	Berón-Vera et al. (2004)
	Uruguay	George-Nacimento et al. (1992)
Steller sea lion (*Eumatopias jubatus*)	USA	Olsen (1958)
Northern elephant seal (*Mirounga angustirostris*)	USA	Dailey (2001)
Southern elephant seal (*Mirounga leonina*)	Crozet Islands (Antarctica)	Johnston and Mawson (1945)
Ringed seal (*Phoca hispida*)	?[a]	Dailey and Brownell (1972)

[a] Location not given

worms in NFS on the Pribilof Islands, especially on SPI. Of special interest was to characterize the biology of the hookworms and study possible control measures to kill larval stages on rookeries. The goal was to reduce morbidity and mortality caused by these parasites in pups.

Olsen (1958) demonstrated several aspects of these parasites: (1) free-living third stage larvae (L_3) did not mature to adults in the intestine of NFS pups, (2) adult hookworms were highly prevalent in NFS and Steller sea lion (SSL) pups but absent in adult NFS (1,426 examined); they only were found in one (a subadult) of 70 older SSL examined, (3) the primary lesions in NFS pups were anemia and hemorrhagic enteritis, (4) either fourth larval stage (L_4) or adult, but not both stages, was found at the same time in the intestines of pups, (5) L_4 were found in young pups (recently born to a few days old) born on rocks washed by the wave action of the Bering Sea, (6) probably the same species of hookworm occurs in NFS and SSL pups but were larger in the latter, (7) Arctic foxes (*Alopex lagopus*) from the same region did not harbor *U. lucasi* but were infected with *Uncinaria stenocephala*, and (8) free-living L_3: (a) overwintered on rookeries but declined during spring and summer, (b) were found on rookery soil in large numbers in late summer and early fall resulting from eggs passed in feces of pups born that season, (c) given orally and percutaneously to NFS and Arctic fox pups did not mature in the intestine, (d) experimentally penetrated through the flipper skin in greater numbers than other areas of the body, and (e) were killed by cresylic acid (5%) sprayed on rookery soil, but this did not result in a decrease of mortality in the pups or prevalence and numbers of adult hookworms in them the next season.

Research in northern fur seals on the Pribilof Islands in the early 1960s and later

Extensive research, concentrating on the biology of hookworms, mainly on SPI, was carried out in NFS in 1960, 1961, and 1962 (Lyons and Olsen 1960, 1962a, 1962b; Lyons 1963; Olsen 1962; Olsen and Lyons 1962, 1965). Some highlights of research by Lyons and Olsen follow. The most significant finding was the discovery of the source of infective stages that mature in the intestine of pups. This was demonstrated by placing pregnant cows in cages either on rookeries or on uncontaminated ground to give birth. The majority of pups born to these females had intestinal infections of hookworms; this showed that the mother was necessary for the infection of her pup. No evidence of prenatal infection was found by examination of tissues of fetal pups and by holding Caesarian section (C-section) pups in captivity for at least 2 weeks, which was the prepatent period of hookworms in natural infections in pups born on rookeries.

Parasitic L_3: (a) were found in milk in the stomach of a pup only 2 h old, in milk from pregnant cows, and a mixture of milk, mammary tissue, and ventral blubber (MMVB) from pregnant cows; (b) were recovered from MMVB from pregnant cows and, after given orally to C-section pups, most developed intestinal infections; this proved that the parasitic L_3 in milk of pregnant cows were infective and the source for the development of adult hookworms in the intestine of pups, (c) were isolated from ventral blubber and/or mammary tissue of NFS nonpregnant cows, 3- or 4-year-old NFS males, and male sea lions; when given orally to C-section pups, this did not result in

intestinal infections, indicating sources of parasitic L_3, other than from pregnant cows, did not mature in pups (Lyons and Olsen 1962b; Lyons 1963; Lyons and Keyes 1978), (d) were recovered from ventral tissues (blubber and/or mammary tissue) of 100% of all ages (except young pups until late August) and both sexes of NFS; but were considered as "dead end" except for pregnant cows which pass them in milk to their pups, (e) are passed in the milk of cows for a short time postpartum, and (f) were observed to overwinter in ventral tissues of pregnant cows.

Free-living L_3: (a) develop to this stage entirely within the egg, (b) total length and width is less than parasitic L_3, (c) administered orally and on the flippers of C-section pups were detected later in the ventral blubber, and (d) found in the blood may have been contaminants from the laboratory equipment.

Summation of life cycle of *U. lucasi* in northern fur seals

Parasitic L_3 pass in the first milk of a cow to her nursing pup and mature in its intestines in about 2 weeks. Eggs are passed in the feces of pups onto the rookery. Free-living L_3 hatch from the eggs, usually beginning in late August. Then, the L_3 enter pups and older seals predominately via penetration of the flippers but also orally; next, they migrate to parenteral tissues, especially ventral blubber (Fig. 1).

These larvae, now called parasitic L_3, do not escape except through the milk of pregnant females. Thus, the only way that adult hookworms can be produced in pups is by transmammary transmission of larvae. This method of infection was the first proven instance of a larval helminth being passed in the milk of a mother and maturing in her offspring. The nursing mother can be considered as an "intermediate host." Lucas (1899) was of the opinion that adult hookworms in pups were acquired while nursing by ingestion of free-living L_3 from rookery soil around the teats of their mothers; his idea was almost correct. After it was discovered that hookworms infect pups by transmammary transmission, trying to prevent or reduce the completion of the life cycle by spraying rookeries to kill free-living L_3 or other methods seemed impractical and not feasible. The great decline in the number of hosts, that is fur seals, may have helped achieve the goal of reduced transmission of these parasites (see more in "Longevity of *U. lucasi* in northern fur seals"). Transmammary transmission seems like a "perfect" method to complete/continue the life cycle of *U. lucasi* because, when a pup nurses an infected cow, it will be infected. However, since free-living L_3 do not mature in pups and since older seals do not have adult hookworms shedding eggs in their feces, only transmammary transmission limits the source of infection, especially when prevalence is low.

After the hookworm life cycle was discovered for northern fur seals, two very early reports were found in the literature of nematode larvae present in a mother's milk. However, the potential significance of their findings was not recognized. One report was of a natural infection of *Trichinella spiralis* in humans (Salzer 1916)

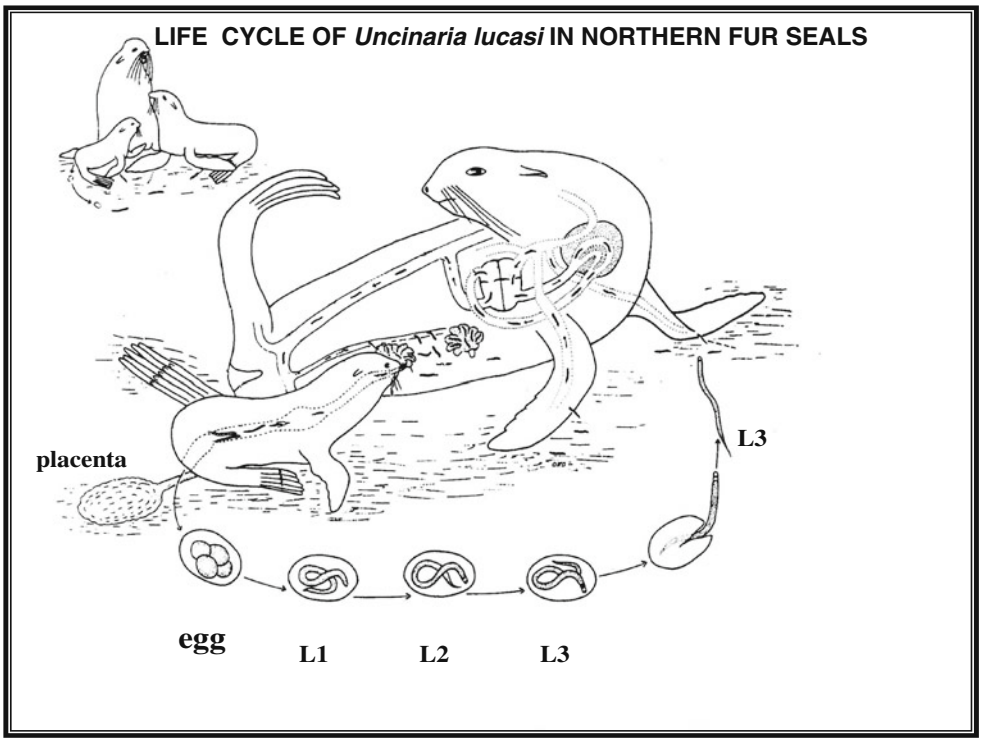

Fig. 1 A newborn pup (note placenta still attached) ingests hookworm larvae (parasitic third stage, *L_3*) in the first milk of its infected mother (cow). This is the only source of larvae developing to maturity in the intestine of a pup. Hookworms mature in about 14 days. Then eggs are passed in the feces of the pup onto the rookery surface. Development to the free-living third stage (*L_3*) occurs within the egg before hatching. These L_3 penetrate the skin or are ingested by all ages (except very young pups) of fur seals; they do not mature in the intestine but migrate predominantly to the ventral abdominal blubber/mammary tissue. Here, the parasitic L_3 are at a "dead end" except in the cow at parturition when they pass in the first milk to her pup and mature in its intestine. (Drawing adapted from Olsen 1962)

and the other report was from an experimental infection of *Ancylostoma caninum* and *Toxocara canis* in guinea pigs (Kotake 1928, 1929).

Since the discovery of transmammary transmission of hookworms in NFS, this phenomenon has been documented for many species of helminths in several hosts (Lyons 1994). Transmission of hookworm larvae through the mammary system has been detected for three pinniped host species besides northern fur seals: (1) Juan Fernandez fur seals, (2) New Zealand sea lions, and (3) California sea lions (Castinel 2006; Sepulveda 1998; Lyons et al. 2003).

Longevity of *U. lucasi* in northern fur seals

Attempts were made to determine how long parasitic L_3 live in tissues of NFS females. Findings include: (a) ventral blubber was positive from 20 of 26 females examined in the Bering Sea during their annual migration to breeding grounds, indicating larvae lived in them for at least 6 months (Lyons and Olsen 1962a; Lyons 1963), (b) three females, captured as yearlings, were taken to Nanaimo, Canada; at 4 years of age, their blubber or pups born to them were positive (Lyons and Bigg 1983), and (c) two females captured as yearlings were taken to the Seattle Aquarium; 6 years later, both gave birth and the pups were positive (Lyons and Keyes 1984). These data show that parasitic L_3 can live and are viable for at least 6 years in blubber.

A study was done to try and determine the period of time that adult hookworms live in the intestines of pups. Data from 1960 and 1961 indicated that pups started losing infections in late August and early September; none was positive after the third week in September. This indicated that adult hookworms persist in the intestines for only a short time, possibly 6 to 8 weeks (Lyons 1963). The finding of this short period of infections of adult hookworms was similar in northern fur seal pups on San Miguel Island; this observation mainly was based on data from the examination of feces for hookworm eggs in live pups (Lyons et al. 2001).

Prevalence of *U. lucasi* in northern fur seals

St. Paul Island, AK

Data, primarily collected in July and August, on adult hookworms in dead NFS pups on one rookery, or combined with another rookery, revealed prevalences of 79% in 1955, 73% in 1960, 90% in 1978, <10% in 1999, 3% in 2001, and 6% in 2007 (Lyons et al. 2000a; Lyons et al. 2003; Ionita et al. 2008). The dramatic decline in prevalence and intensity of adult hookworms in pups was reflected in a similar decrease in the number of young males (3 to 4 years old) positive for parasitic L_3 in their blubber. It seems probable that the current low prevalence is associated with the parallel tremendous reduction in fur seal numbers. This means that because so few pups are infected and passing hookworm eggs onto the rookery, the level of "recycling" of these parasites is low. With so many fewer fur seals, one change in breeding areas on St. Paul Island from years ago is that more rookeries are located on rocky areas near the sea. When there were much higher numbers of breeding seals, harems extended well back from rocky areas onto sandy habitat that is much more suitable for hookworm transmission. In addition to density-dependent factors, another hypothesis is that the major histocompatibility complex (MHC) genes present in the population may be more effective in creating immune responses that resist hookworm infections (DeLong 2007).

San Miguel Island, CA

Several studies have been conducted on NFS on San Miguel Island (SMI). The most extensive research began in 1996 and has continued periodically since then (Lyons et al. 1997, 2000b, 2001, unpublished data for 2005 and 2008). These studies involved examination of dead pups by necropsy, primarily in July and August. This is the peak period of hookworm transmission and maturation in the intestines of pups. All pups, except one, harbored adult hookworms in their intestines. The number of individual worms ranged from a few to several thousand per pup. Fecal samples examined from live pups in late September and October revealed all were negative for hookworm eggs (DeLong 2007). These data paralleled findings for dead pups on St. Paul Island, where adult hookworms were not found in these hosts after mid-September, indicating that adult hookworms persist for only a short time, possibly 6 to 8 weeks in NFS pups. As mentioned by DeLong (2007), prevalence of hookworms in NFS pups on San Miguel Island is known from adult worms found in dead pups in July and August and from eggs in feces from live pups in the fall. The only information on prevalence in live pups during the summer months was finding 83% of 30 pups shedding eggs in feces in August 2006 (DeLong et al. 2009).

Another aspect on the prevalence of hookworms included research in 2003, 2005, and 2008 which included the examination of the peritoneal cavity for adult hookworms in NFS pups (Lyons et al. 2011 and unpublished data). Numerous pups were infected in this abnormal anatomical location. The stimulus for this observation was the report of adult hookworms penetrating through the small intestinal wall into the peritoneal cavity of a California sea lion (*Z. californianus*) pup on San Miguel Island (Spraker et al. 2004)

Studies in Russia

Numerous studies have been performed on *U. lucasi* in northern fur seals on Russian islands. The most extensive research has been by Kolevatova et al. (1998, 2004). Their studies included various biological aspects of hookworms including life cycle, prevalence, ecology, and treatment. Kato (1997) and Mizuno (1997) included descriptions of several facets of the life cycle, pathology, and prevalence. Some of the dead pups on Russian rookeries harbored more than 1,600 hookworms (Mizuno 1997). Starostin (1973) reported the highest mortality of pups was between mid-July and mid-August.

Pathology of hookworms and related mortality in northern fur seal pups

The first recorded history of damage caused by pinniped hookworms was by Lucas (1899) in dead NFS pups on the Pribilof Islands. Some of his descriptions at necropsy were: hookworms found and identified as *Uncinaria* spp., paleness of the "flesh"; also of the lungs and kidneys in some cases, anemia, reddish cyst-like spots caused by attachment of the hookworms in the intestines, "little" blood which may be thin and watery. The intestinal wall appeared to be thickened. His necropsies showed for the first time that, not only hookworms were present in pups, but that they can be a major cause of death of fur seal pups. Some later examinations of NFS pup pathology were by (Brown et al. 1974; Doyle 1957; Keyes 1965), but they did not add significant information to that already reported by Lucas (1899).

Recent studies in regard to the lesions caused by hookworm disease have shown two different patterns (Spraker and Lander 2010). The most common lesion in NFS pups is a chronic anemia in a fairly well-nourished pup. Gross lesions also included a moderate hemorrhagic enteritis characterized by multifocal regions of a red thickened intestinal wall, multifocal small pale areas in the liver, and occasionally a dilated, enlarged heart. The lumen of the small intestine contained blood. These lesions characterize those found in NFS pups on SPI. In contrast on SMI, NFS pups have this suite of gross and histological lesions, but also have lesions where hookworm penetration of the wall of the small intestine and cause peritonitis and bacteremia similar to what has been described in CSL (Spraker et al. 2004, 2007; Lyons et al. 2011).

DeLong (2007) has reported the current mortality status associated with hookworms in *C. ursinus* pups. He indicated that mortality is minimal for pups on the Pribilof Islands, Kurile Islands, and Robben Island. Some hookworm-induced mortality exists for pups on the Commander Islands (Bering Island and Medney Island); hookworms are a major cause of death of pups on San Miguel Island, which is one of the California Channel Islands.

Treatment of hookworms in northern fur seal pups

Several chemical compounds have been evaluated for the removal of adult hookworms in NFS pups. Dichlorvos (pellet and tablet formulations) was highly effective although it may have contributed to the death of a single pup treated with the pellet formulation (Lyons et al. 1978; Bigg and Lyons 1981); disophenol had varied activity (Lyons et al. 1978, 1980). Ivermectin has been shown to have excellent activity on pinniped hookworms. It was tested in NFS pups on St. Paul Island (Beekman 1984) and by DeLong et al. (2009) on San Miguel Island. DeLong et al. (2009) found that, besides the high removal of hookworms by ivermectin, the growth and survival of the treated pups was much greater than that of nontreated control pups. Ivermectin also has been reported as highly active on hookworms in New Zealand sea lion pups (*Phocarctos hookeri*) (Castinel 2006; Chilvers et al. 2009). Russian parasitologists (Kolevatova et al. 1998) treated hookworm-infected fur seal pups with diethylcarbamazine, fenbendazole, levamisole, and morantel tartrate, with levamisole proving the most effective.

Species of *Uncinaria* in non-pinniped hosts

A related species of hookworm, *Uncinaria stenocephala*, found especially in canids (Anderson 1992), has several characteristics different from those of *Uncinaria* spp. in pinnipeds. Some of them are: (1) all ages of the host may harbor adult hookworms in the intestines, (2) intestinal infections of adult hookworms are derived mainly from free-living L_3 ingested from the environment but can be from ones penetrating the skin (Gibbs 1961), and (3) prenatal or transmammary transmission apparently does not occur (Bowman et al. 2003), although a very low number of larvae has been reported in the milk of dogs (Walker and Jacobs 1982).

Concluding remarks

The life cycle of hookworms and breeding habits of northern fur seals (probably other pinniped hosts also) are "synchronized." Parturition and lactation of larval hookworm-infected cows are necessary to perpetuate these parasites. The source of infection of adult hookworms in pups is from a reservoir of parasitic L_3 that may live in tissues of cows for many years and pass in the milk to their offspring after parturition. It is essential for pups to pass

hookworm eggs in their feces, from which free-living L_3 develop on rookeries and enter tissues of the seals to maintain the parasitic life cycle.

Research on the hookworm *U. lucasi* in northern fur seals resulted in advancing knowledge, not only on the biology of hookworms in pinnipeds, but also on internal parasites in other hosts. The discovery of the transmammary transmission of these parasites to fur seal pups led to the consideration of this mode of transmission for other parasites. It is now recognized that transmammary transmission is not uncommon for helminth parasites.

Studies in later years on fur seals on St. Paul Island showed the tremendous decline in the prevalence of hookworms. This may be related to the huge decrease in the number of fur seals resulting in perturbation of the hookworm transmission; also, MHC may be a factor. The prevalence of hookworms is still high in pups on SMI, and these parasites are a major cause of mortality in pups.

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