



The life history strategy of a fur seal hookworm in relation to pathogenicity and host health status



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ABSTRACT

The strategies that parasites use to exploit their hosts can lead to adverse effects on human and animal populations. Here, we describe the life cycle, epidemiology, and consequences of hookworm (*Uncinaria sp.*) disease in South American fur seals (*Arctocephalus australis*), and propose that hookworm adaptation to fur seal life history traits has led to maximizing transmission at high levels of parasite-induced anemia and mortality. Fur seal pups acquire hookworms during their first days of life through their mothers' colostrum and most adult hookworms are expelled from the pups' intestine 30–65 days later. This gives hookworms little time to feed and reproduce. However, despite reaching high within-host densities, female hookworms do not decrease egg output, therefore pups with high hookworm burden contribute disproportionately to parasite egg shedding. These heavily infected pups also suffer severe anemia and high levels of hookworm-induced mortality. Alternative strategies to maximize total egg shedding and/or transmission, such as increased environmental survival of larval stages or avoidance of clearance, have not been developed by this hookworm. We propose that fur seal hookworms exploit a live fast-die young life history strategy, which translates to the highest levels of host anemia and mortality recorded among hookworms.

1. Introduction

Soil transmitted helminths are one of the most prevalent and detrimental parasitic infections in the world, with substantial resources deployed for their control and eradication (Bartsch et al., 2016; Jourdan et al., 2017). Within this parasite group, hookworms are particularly pathogenic because they establish long-lasting infections and exhibit a detrimental feeding behavior for the host (Bartsch et al., 2016). With the help of well-developed buccal plates and secretion of several anticoagulant proteins, hookworms cause bleeding wounds in the intestine in order to feed on host blood (Loukas et al., 2005). Therefore, in human and animal populations affected by these parasites, intestinal bleeding and chronic regenerative anemia are the hallmarks of infection (Bartsch et al., 2016; Jourdan et al., 2017; Seguel and Gottdenker, 2017). Additionally, because of the extraction of blood and loss of protein through the intestine, hookworm infection has been associated with retarded growth in human and wild animal populations

(Bartsch et al., 2016; Seguel and Gottdenker, 2017).

Despite these adverse consequences for host health, hookworm-induced mortality is rare in humans and animals, with the exception of pinnipeds (seals, fur seals and sea lions) (Bartsch et al., 2016; Seguel and Gottdenker, 2017). In pinnipeds, and most specifically otariids (eared seals), hookworms (*Uncinaria sp.*) can cause up to 70% of the total pup mortality during a reproductive season (Spraker et al., 2007; Lyons et al., 2011; Seguel and Gottdenker, 2017). The reasons for these high levels of mortality among eared seals are unknown, but in several otariid species, parasite prevalence and burden are the most important factors driving host mortality (Castinel et al., 2007; Spraker et al., 2007; Lyons et al., 2011; Seguel and Gottdenker, 2017; Seguel et al., 2017). For instance, most necropsied South American fur seal pups (SAFS, *Arctocephalus australis*) at Guafo Island (Chilean Patagonia), are infected with an undescribed *Uncinaria sp.* but only animals with high burdens die due to a combination of hookworm lesions and secondary bacterial infection of these wounds (Seguel et al., 2017).

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For a soil transmitted nematode, pinniped hookworms (*Uncinaria* sp.) have been quite successful in a coastal environment that poses challenges to their survival. Most pinniped hosts form large aggregations along shores during the reproductive season, yet they spend most of their time in the ocean (Paves and Schlatter, 2008). Additionally, many pinniped rookeries are located in latitudes subjected to extreme temperatures and constant wash of sea and rain water (Castinel et al., 2007; Lyons et al., 2011; Seguel et al., 2013). Therefore, pinniped hookworms likely developed alternative strategies to cope with challenges to their survival and reproduction, resulting in high levels of mortality in many marine mammal populations. Some of these strategies, for instance, could be related to increased resistance of larval stages in the environment, prolonged egg shedding in the definitive host (prolonged infectious period) and/or alternative modes of transmission of infective stages. However, studies in several otariid species suggest that the life cycle of marine hookworms is similar to terrestrial carnivores, except that transmission of infective larvae is exclusively lactogenic (Olsen and Lyons, 1965; Lyons et al., 2011). This suggests that marine hookworms could have attained high prevalence among otariids due to synchronization with the host reproductive cycles, although increased opportunities for transmission through environmental resistance of larval stages and/or prolonged egg shedding are potential contributory factors.

In this manuscript, we describe the life cycle and epidemiology of *Uncinaria* sp. infection in South American fur seals (SAFS, *Arctocephalus australis*) using field data and experiments in order to understand the dynamics of hookworm transmission in pinnipeds within the context of high levels of parasite induced mortality. Additionally, the host population dynamics were compared with that of the parasite to detect if synchronization with host reproductive cycles is feasible. Later, to better understand this hookworm life history strategy in relation to their pinniped host life history, we observed egg production in hookworm females and performed experiments to evaluate hookworm larvae environmental survival. Finally, we measured hookworm-specific mortality and anemia in fur seal pups, and examined the total contribution to hookworm egg shedding in pups that suffered the worst health consequences of parasitism compared to pups that were barely affected by hookworms. Based on this approach, we propose that pinniped hookworms exploit a live fast-die young life history strategy that results in few limitations on extraction of host resources and the highest recorded levels of anemia and mortality among hookworms.

2. Materials and methods

2.1. Study site and animal handling

The study was performed in the reproductive colony of SAFS located at Guafo Island, Northern Chilean Patagonia (43° 35' 34.9" S, 74° 42' 48.53" W) (supplementary figure 1). This rookery, of approximately 3000 individuals during the reproductive season, is located over a mix of sandy and rocky substrates. Pups captures and recaptures were performed in a rookery sector covered by a thin (3–10 cm) layer of sandy soil with moderate amount of organic matter over a rocky substrate (supplementary figure 2).

During 2014 (n = 201) and 2015 (n = 206), 1 to 7 day-old pups were captured by hand and physically restrained. Age of pups was exactly known or estimated using the peak parturition date for Guafo Island (December 15th) and by assessing the rests of placenta and umbilical cord in these young pups (Paves and Schlatter, 2008; Seguel et al., 2016). Placenta is usually loss between 24 and 48 h after birth and rest of umbilical cord are loss between day 2 and 5 (Paves and Schlatter, 2008). The exact age of a subset of pups (n = 20) was known because their birth was observed and they were marked 24 h later.

In each capture, pups were measured, weighed, and blood and fecal samples collected as previously described (Seguel et al., 2016). All pups were marked with correlative numbers using a commercial hair

decolorant applied on the fur.

Each year, a randomly selected group of 30 pups, 10 of them of exact known age (1–2 days old), were treated in their first capture with 400 µg·kg⁻¹ of subcutaneous Ivermectin (antiparasitic drug, control group) (Delong et al., 2009). Half of these pups (n = 30) could be monitored throughout the whole study period and were included in the final data sets.

The pups were recaptured and the sampling procedure repeated on each pup every 5–10 days during the duration of the study (10 weeks) and only pups that were captured at least 4 times were included in the study (76 in 2014 and 73 in 2015).

2.2. Parasitological examination

Due to the lack of standardized methods to obtain a regular amount of feces from pinniped pups and calculate the number of hookworm eggs per gram (in part due to the semiliquid consistency of pup feces), a semi-quantitative protocol of hookworm egg counting was developed. A fecal swab was collected from each pup and placed in a 10 ml tube filled with Sheather's sucrose (1.275 specific gravity). In the field laboratory the swabs were removed from the tubes and additional Sheather's sucrose was added to the tube to obtain a raised meniscus. A glass cover slip was placed on top of the tube and after 1-h flotation placed on a glass slide and observed at 50X magnification with an optic microscope. The area containing more aggregates of hookworm eggs was selected and observed at 100X. Starting from this point the eggs were counted in 10 successive, random microscopic fields and the total number in the 10 fields recorded. This same coprological examination protocol was performed on 48 live captured adult female SAFS and in fecal samples (by embedding the swab in fresh feces) from 58 subadult and adult male SAFS.

To determine if the fecal egg count was a good estimate of nematode burden, the standardized fecal egg count protocol was applied to recently dead pups (n = 33). Necropsy was performed on these pups and nematodes recovered, counted, sexed and identified as previously described (Seguel et al., 2011, 2017). In addition, between 2004 and 2017 a total of 15 adult SAFS females and 26 adult SAFS males were necropsied and carefully examined for presence of metazoan parasites.

In order to determine the average number of eggs per hookworm female, randomly selected hookworm females (n = 50) and males (n = 50) from each host (necropsied pups) were measured (standard body length and width), and females body wall was macerated by placing them in sodium hypochlorite solution (0.5%) to extract all the eggs from the female's uterus. Eggs were recovered using a 38 µm sieve and suspended in a standard volume of saline solution (NaCl 0.9%). Eggs were counted 3 times using a graded chamber with 1000 µl capacity. The average of the 3 counts was recorded and the number of eggs per females calculated based on the total volume of the hookworm egg solution and the number of females macerated (Hussey and Barker, 1973). The same protocol was repeated using different numbers of females from the same sample (25, 10, 5, 1), however no significant differences were detected in the calculated number of eggs per female. Therefore, the same protocol was applied to samples with small hookworm burden using 5, 10 or 25 females per test.

In 2014, 2015 the soil from different sectors of the rookery was collected. A sector of the rookery was divided in 100² m quadrants and 5 collection sites were randomly selected within each quadrant (supplementary figure 3). Sampling was conducted in 5 quadrants in early December and in the same quadrants and other additional 15 quadrants through mid and late January of each year. All collection sites were located at least 10 m from the high tide line, because at Guafo Island, areas with surf wash do not contain soil but large rocks. A standard volume (50 ml) from a homogenized subsample of soil from each collection site underwent Baermann's test for detection of soil nematodes using methods described by Olsen and Lyons (1965) in Northern fur seals (*Callorhinus ursinus*). These included addition of a few drops of

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