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ANIMAL SCIENCE

Effect of host age, sex and life stage on the prevalence and abundance of sucking lice on Weddell seal in the Antarctic Peninsula

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Abstract: Through evolutionary time, seal lice have developed morphological, behavioral, and ecological adaptations to cope with the amphibious lifestyle of their hosts in a co-evolutionary process. Consequently, the dynamics of lice populations are determined by seals behavior. We aim to study the effects of host sex, age class, year, and sampling location, on the prevalence and mean abundance of *Antarctophthirus carlinii,* on Weddell seals (WS) *Leptonychotes wedelli*. The study was conducted at two sites in the Antarctic Peninsula, namely, Marambio/Seymour Island (MI) and the Danco Coast (DC). We collected lice from 71 WS: 33 from MI, during the reproductive season, and 38 from DC, during the molting season, between 2014 and 2017. According to our analyses, host age class and sex were the variables that affected prevalence levels of lice on WS. Whereas, age class, year, site, and sex affected lice mean abundance. Juveniles presented higher prevalence and mean abundance than adults, possibly acting as reservoirs for lice as they move through different colonies until they reach reproductive age. Concurrently, seals during molting season were more infested. Unlike nursing, during the molting season seals spend much time ashore forming mixed groups that favor both egg development and lice transmission.

Key words: *Antarctophthirus carlinii*, infestation parameters, GLM, *Leptonychotes weddellii*.

INTRODUCTION

The Weddell seal (*Leptonychotes weddellii*) is the southernmost distributed seal and the only pinniped species inhabiting sea-ice during the whole year (Burns & Kooyman 2001). Like all pack-ice seals, Weddell seal distribution is influenced by the availability of haul-out sites in fast-ice. Fast-ice provides a stable substrate for giving birth, nursing pups, and resting (Siniff et al. 2008, Southwell et al. 2012, Thomas & Terhune 2009). Some individuals maintain ice holes throughout the winter while others frequent the offshore pack ice or forage areas, returning to rest on the fast-ice (Thomas & Terhune 2009). This variability in haul-out behavior may have a strong impact on the population dynamics of seals ectoparasites. When hosts move from sea to haul-out sites, ectoparasites get exposed to drastic changes in humidity, pressure, temperature, and solar radiation (Thompson et al. 1998), which could affect and model their population.

The family Echinophthiriidae (Phthiraptera, Anoplura) includes species that infest pinnipeds and the Northern river otter, hence, i.e. they have amphibious hosts who regularly perform long excursions into open sea (Durden & Musser 1994a, b). Through evolutionary time, echinophthiriids have developed unique morphological, behavioral, and ecological adaptations to cope with the marine lifestyle of their hosts (Murray 1976, Mehlhorn et al. 2002, Leonardi et al. 2012, Leonardi & Palma 2013, Leonardi & Lazzari 2014). Moreover, echinophthiriids are of the few insects adapted to survive at sea (Leidenberger et al. 2007, Leonardi et al. 2020).

Some physiological adaptations from *Antarctophthirus carlinii* (Leonardi et al. 2014), the Weddell seal louse, were described by Murray et al. (1965). This louse can become active and breed at 5-15°C; its eggs can develop and hatch at constant temperatures as low as 0-4°C (Murray et al. 1965). However, eggs do not survive submerged, which constitutes the main life history restriction of echinophthiriids as parasites of amphibious hosts (Leonardi & Lazzari 2014). Murray et al. (1965) also found that infestations spread would occur solely from female seals to their pups by the transference of adult lice, and was more frequent and heaviest on yearling and immature seals than on mature seals. The life cycle of *A. carlinii* lasts approximately 3-4 weeks. Hence, lice reproduction could only occur when their hosts remain on land for enough time. Therefore, the number of lice generations per year would be constrained by the duration of haul-out periods of their hosts. In this sense, the inter and intraspecific variations in the time spent by individuals hauling out to rest, molt, or breed would influence the dynamics of echinophthiriid lice (Thompson et al. 1998, Aznar et al. 2009). Moreover, environmental conditions could modify host behavior and, consequently, lice population dynamics, resulting in geographical and/or annual variations in the host-parasite association (Thompson et al. 1998).

We aim to study the effects of host sex and age class, as well as the year and sampling location, on the prevalence and mean abundance of *Antarctophthirus carlinii,* which infest Weddell seals (WS) *Leptonychotes wedelli* in two places of the Antarctic Peninsula, that is, Marambio/Seymour island (MI) and the Danco Coast (DC) (Figure 1). Based on the premise

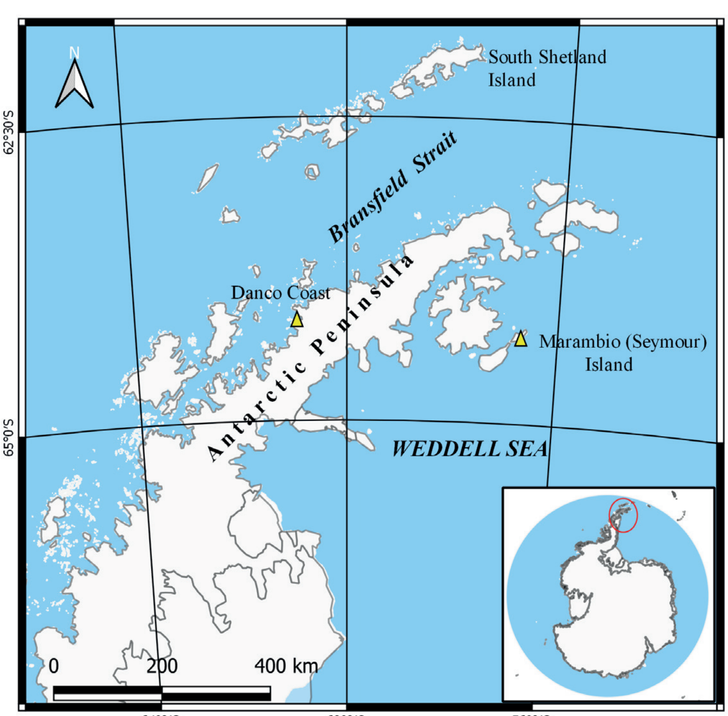

Figure 1. General view of Antarctica. Antarctic Peninsula. Marambio/ Seymour Island, (reproductive site) and the Danco Coast (molting site).

that the population dynamics of *A. carlinii* is determined by seal behavior, we propose that infestation parameters such as prevalence and mean abundance would vary according to the site and the stage of the seals' life cycle.

Abbreviations

Weddell seals WS
Marambio/Seymour island MI
Danco Coast DC

MATERIALS AND METHODS

The study was conducted at Marambio (Seymour) Island during the reproductive seasons and at Danco Coast during the molting seasons of 2014, 2015, 2016, and 2017 (Figure 2). Lice were collected from the hind flippers of seals following Thompson et al. (1998) and preserved in 96% ethanol. The hind flippers are the preferred area for lice and the numbers collected there are a reliable proxy of the total burden, reducing in this way manipulation time (Thompson et al. 1998, Leonardi 2014). Once in the lab lice were classified as adults (females and males) and nymphal stages.

Determination of host age class and sex was performed by visual inspection of external characteristics and body size was estimated for each sampled seal.

Modeling Infestation Parameters

Prevalence

Given that prevalence is defined as the proportion of infested hosts in the population, this parameter was modeled as the probability of a host having at least one lice. Hence, prevalence is the success parameter for each trial following a Bernoulli distribution. Where y_i is a random variable taking values of 1 if the *ith* individual is infested or zero if the individual is not infested. The effects of the age class, sex, site, and year on the prevalence were investigated using a linear model from a logit link function transformation.

Mean Abundance

Following the mean abundance definition as the mean number of parasites per host in the population, a Poisson distribution is an appropriate choice for modeling the individual data. However, given the overdispersion observed in the data, a negative binomial distribution was used for investigating the effect of the above mentioned factors. The random variable, in this case, was defined as the number

Figure 2. a) Weddell seal on Marambio/Seymour Island during the reproductive season. **b)** Weddell seal in the Danco Coast during the molting season.

of parasites observed in each host. The effects of the age class, sex, site, and year on the mean abundance were investigated using a linear model from a log link function transformation.

Parameters estimations and model selection

We proposed a set of 19 and 18 competing models for studying the effect of the age class, sex, year, and sites on the prevalence and mean abundance, respectively. Parameters estimations was maximum likelihood-based and the model selection procedure was carried out using the small sample corrected Akaike Information Criterion (AICc) (Akaike 1985, Hurvich & Tsai 1989). The best-supported model by the data was chosen following Burnham & Anderson (2002). All analyses were performed using open-source software R version 3.6.1 (R Core Team 2019).

RESULTS

We sampled 71 Weddell seals: 33 from Marambio/Seymour Island and 38 from Danco Coast. Infestation parameters of *A. carlinii* collected from Weddell seals, are shown in Table I.

We investigated the effects of host age class, sex, year, and site on the prevalence and mean abundance by a generalized linear model formulation.

Prevalence

The best model based on AICc included age class and sex as explainatory variables that affect the prevalence levels of *A. carlinii* in *L. weddellii* (Table II). Given the best-supported model, the estimated prevalence was higher in juveniles (42.3%) than adults (7.5%) (p = 0.0046). Although factor sex was part of the best model, no differences were observed between males and females (p = 0.5991) (Figure 3).

Mean abundance

The best-supported model showed the effect of age class and the interaction between site and sex on the mean abundance (Table II). The estimated mean abundance was higher in juveniles (4.53) than adults (0.93) (p = 0.0002) (Figure 4). There was a significant interaction between sex and site (p = 0.0173). For males, differences between sites were not detected with 2.88 and 2.83 lice per host for Danco Coast and Marambio/Seymour Island respectively (Figure 5). However, the estimated mean abundance for females was higher in individuals from Marambio/Seymour island than from Danco Coast (p = 0.0173) with 3.17 and 0.39 lice per host, respectively (Figure 5).

Table I. Total number of hosts analyzed (n), infestation parameters and standard deviation (in parenthesis) for *Antarctophthirus carlinii* from Weddell seals by host sex and age class, year, and site.

	Females	Males	Adults	Juveniles	2014	2015	2016	2017	Danco Coast	Marambio/ Seymour Is.
n	**35**	**32**	**44**	**26**	**18**	**31**	**12**	**10**	**38**	**33**
Prevalence %	14.3 (35.5)	28.1 (45.7)	9.0 (29.1)	42.3 (50.4)	33.3 (48.5)	6.4 (24.9)	33.3 (49.2)	30 (48.3)	23.7 (43.1)	18.2 (39.2)
Mean Abundance	1.6 (3.8)	2.6 (3.9)	1.1 (3.7)	3.8 (4.2)	3.5 (5.3)	0.8 (2.0)	2.9 (4.0)	2.3 (3.8)	2.5 (4.3)	1.6 (3.1)
Mean Intensity	5.1 (5.4)	5.2 (4.2)	3.4 (4.9)	6.2 (3.7)	5.8 (5.8)	3.2 (2.9)	5 (4.1)	5.7 (4.0)	5.6 (4.9)	4 (3.9)

Table II. Model selection results for competing models proposed for effects of host sex, age class, year, and sites on the prevalence and mean abundance of *Antarctophthirus carlinii* on Weddell seals in the Antarctic Peninsula. In bold the best-supported model. AICc: Akaike Information Criterion corrected for small sample size; ΔAICc, is the difference between the lowest AICc value (i.e. best of suitable models) and AICc from all other models.

Infestation Parameter	Model effects	AICc	ΔAICc
PREVALENCE	**Age_Class + Sex**	**62,81**	**0**
	Age_Class + Sites * Sex	63,18	0.37
	Age_Class + Year	63,61	0.80
	Sites + Age_Class * Sex	65,46	2.64
	Age_Class	66,41	3.59
	Sites * Age_Class	66,60	3.78
	Age_Class * Year	67,23	4.41
	Year + Sex	70,80	7.98
	Sex	70,90	8.09
	Sites + Sex	72,66	9.84
	Sites * Sex	73,63	10.82
	Year	73,84	11.02
	Sites + Year	74,44	11.62
	Year * Sex	74,64	11.82
	Sites	77,07	14.25
	Sites * Year	77,26	14.44
	Age_Class * Sex	86,80	23.98
	Sites + Age_Class	91,12	28.306
	Null Model	97,29	34.47
MEAN ABUNDANCE	**Age_Class + Sites * Sex**	**224.27**	**0**
	Age_Class + Sex	230.19	5.93
	Age_Class * Sex	232	7.73
	Sex	235.06	10.8
	Sites + Sex	235.32	11.05
	Sites * Sex	235.34	11.07
	Year + Sex	236.28	12.01
	Year * Sex	238.27	14
	Age_Class + Year	239.85	15.58
	Age_Class * Year	240.47	16.21
	Sites + Age_Class	242.65	18.38
	Sites * Age_Class	243.24	18.97
	Age_Class	245.72	21.46
	Sites + Year	250.84	26.57
	Year	251.6	27.33
	Null Model	251.66	27.39
	Sites	252.88	28.61
	Sites * Year	255.3	31.03

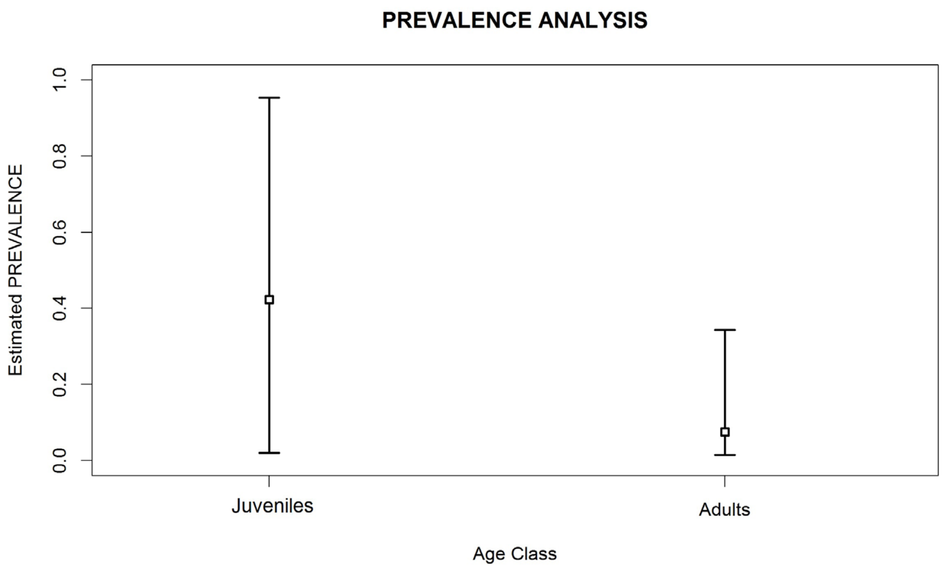

Figure 3. Estimated prevalence for both juvenile and adult Weddell seals under the best-supported model. Verticals bars represent the 95% confidence interval of the estimated infestation parameters.

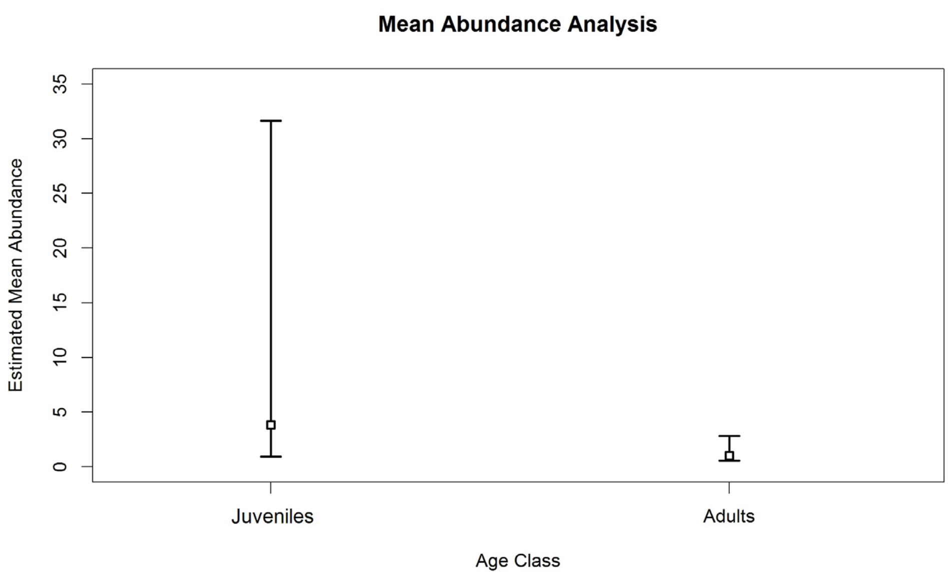

Figure 4. Estimated mean abundance for both juvenile and adult Weddell seals under the best-supported model. Verticals bars represent the 95% confidence interval of each estimated infestation parameter.

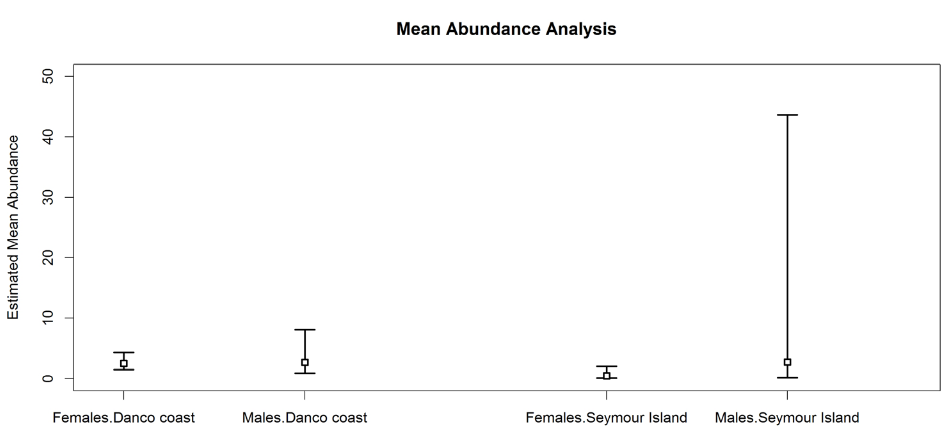

Figure 5. Estimated mean abundance for the four treatments observed for the interaction between sex (males and females) and site (Marambio/ Seymour Island and Danco Coast) under the best-supported model. Verticals bars represent the 95% confidence interval of each estimated infestation parameter.

DISCUSSION

We studied for the first time how the population dynamics of an echinophthiriid louse is influenced by host behavior, analyzed at an annual and life stage scale. Our results show that the prevalence of *Antarctophthirus carlinii* on Weddell seals mainly depends on the host age class and sex. While mean abundance depends on host age class and the interaction between site and sex.

Our models indicated that juveniles present higher prevalence and mean abundance than adults. A possible explanation could be that juveniles typically move through different colonies in the open pack-ice until reaching their reproductive age. While adult seals often returned to the same colony, showing a high degree of site fidelity (Stirling 1969, Stirling & Greenwood 1972, Davis et al. 2000). In this sense, density-dependent mechanisms or the dynamic of each colony could affect the dynamic of lice infestation.

Regarding the effect of site on the infestation parameters, we observed that seals during the molting season (Danco Coast) were more infested than those sampled during the reproductive season at Marambio/Seymour Island. This could be related to differences in the behavior of individuals between the two phases of the life cycle. For instance, during the reproductive season seals do not spend much time ashore (Stirling 1969). In fact, during lactation adult females make foraging trips and their pups start to get into the water a few weeks after birth (Cameron & Siniff 2004). Also, during the pupping season, seals are spaced in the pupping colonies and nonbreeding seals and subadults are excluded from these areas (Stirling 1969). While during the molting season seals spend more time ashore, forming mixed groups of males, non-pregnant females, juveniles, and pups (Bengtson et al. 2011, Stirling 1969). Indeed, we observed those mixed groups resting on the beach in Danco Coast (personal observation). Furthermore, the local environment may also influence behavior since Weddell seals tend to haul out more under conditions of low wind speed and higher temperatures while they remain submerged when it is windy and cold (Andrews-Goff 2010). Weddell seals at Marambio breed in early spring when there is a prevalence of strong and cold winds (mostly from the SW) in the area and a mean temperature that ranges from –15.1ºC in June to -1.7ºC in December (Marambio Weather Station SMN) while at Danco Coast, the average temperature during the summer months is usually above -2°C and days with intense winds are rare. As we mentioned before, temperature influenced both egg development and lice mobility. Consequently, the higher temperature and longer time ashore at the Danco Coast would favor both reproduction and lice transmission.

Previous studies suggest that the infestation patterns on echinophthiriids would be related mainly to the host age, being higher in younger individuals. In this sense, the prevalence and intensity of *Echinophthirius horridus* on the harbour seal vary with host age but not sex, being higher on immature seals (Thompson et al. 1998); a similar pattern was described for *A. lobodontis* from the juveniles of *Lobodon carcinophaga*, during moulting season (Soto et al. 2020); and for pups of Southern sea lions (Aznar et al. 2009, Leonardi et al. 2013), and the Northern fur seal (Kim 1975). However, as was mentioned before, for *A. carlinii* we detected the influence of the host age on the prevalence and mean abundance, but also other factors as host sex, and site and year of sampling. More studies on other pinniped-lice systems are needed in order to understand if the infestation parameters of seal lice respond to a general pattern.

Until now, the only work that studied this lice-host interaction was that from Murray et al. (1965). They proposed that transmission of *A. carliniii* occurs from adult females to their pups and that only adult lice are transmitted, being yearling and immature seals more infested than mature seals. Here we found that juveniles would be the main spreaders and are more infested than adults. In this work we did not study *A. carlinii* adaptations or strategies to survive on Weddell seals, yet, we propose that one of *A. carlinii* transmission strategies could be through mobility of adult females, in order to complete a generation in a short period of time. Nevertheless, we think that further studies are needed to know more about such transmission strategies.

Fast-ice areas show high variability among years (Fraser et al. 2012). As Weddell seals use fast-ice for reproduction, a reduction in the availability of this substrate leads to fewer seals hauling out to reproduce (Stirling & Greenwood 1972, Siniff et al. 2008). As shore ice disappears seasonally, the seals move into the pack ice, moving back as close to the coast as possible only when the coastal ice refreezes (Ainley et al. 2015). Thus, any variation in the environment may affect the infestation parameters. Hence, long-term analyses focused on this host-parasite interaction in a highly changing environment as Antarctica is needed to understand how lice, through coadaptation and coevolution mechanisms, respond to their host life history and behavior.

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