

Tell me who you go with and I will tell you what you do: Antarctic seal lice behave differently

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Abstract

Lice of the family Echinophthiriidae are obligate and permanent ectoparasites of pinnipeds and sea otters. Morphological, ecological, and behavioral adaptations have enabled them to survive in their amphibian hosts. However, it has been shown experimentally that the eggs do not survive submerged. This physiological limitation restricts their reproductive events to the terrestrial periods of their hosts, mainly during molting and reproduction. We studied the reproductive strategies of *Antarctophthirus lobodontis* on crabeater seals (CS, n = 54) and *A. carlinii* on Weddell seals (WS, n = 54) from Danco Coast, Antarctic Peninsula, during the molting season. Lice were sexed and classified as adults or nymphs under a stereomicroscope. The 20.37% of the CS had potentially viable eggs and all the nymphal stages and adults. However, in the WS we only found N3 and adults. Our results would suggest that *A. lobodontis* lays viable eggs that can survive immersion. Instead, the transmission of *A. carlinii* would be mainly by adults. According to previous studies, *A. carlinii* would reproduce during the reproductive season of WS. These reproductive strategies of seal lice would be related to the life history of their host, mainly to diving behavior and the haul-out patterns during their life cycle, reflecting the strong coadaptation and coevolution mechanisms between seals and lice. The differences in the population structure of the two species observed here may indicate that they are different species, or at least that they have undergone different co-evolutionary processes depending on the habit of their hosts.

Introduction

Pinnipeds, i.e. sea lions, seals, and the walrus, are infested by a particular group of sucking lice, the echinophthirids (Anoplura: Echinophthiriidae) (Kim 1971; Leonardi et al. 2021). These lice are peculiar by their behavioral, ecological, morphological, and/or physiological adaptations to the amphibious life of their hosts (Kim 1971; Murray 1976; Leonardi et al. 2021). Furthermore, they are among the few insects that have been able to adapt to the marine environment (Leonardi et al. 2021). They are permanent and obligate ectoparasites throughout their whole life cycle (Fig. 1) which includes eggs, nymphs (three instars) and adults (female or male) (Murray and Nicholls 1965; Kim 1971). Vertical transmission, from female seals to their pups, appears to be the main way of transmission in seal lice (Murray et al. 1965; Leonardi et al. 2013; Soto et al. 2022).

The long evolutionary history they share with their hosts has exposed them to selective pressures. As a result, they show specific adaptations that allow them to tolerate long and deep immersion periods (Leonardi et al. 2021). However, as terrestrial insects, their reproduction remains tied to the land. One of the major constraints for seal lice is that their eggs do not survive submerged (Murray et al. 1965; Leonardi and Lazzari 2014). Reproductive events are therefore limited by the duration of their hosts' haul-out periods, which occur mainly during the breeding and molting periods of the seals (Aznar et al. 2009; Leonardi et al. 2013). In other words, lice adjust precisely their reproductive events to the life cycle of their host (Murray and Nicholls 1965; Murray et al. 1965; Kim 1971, 1972, 1975; Aznar et al. 2009; Leonardi and Lazzari 2014). Therefore, the reproductive events and the number of lice generations depend on the biology and ecology of their host (Leonardi et al. 2013).

In the case of pack ice seals, they depend on sea ice to molt and reproduce, and alternate periods of haul-out resting with periods of feeding (Gilbert and Erickson 1977; Erickson and Hanson 1990). For instance, crabeater seals are pelagic feeders (Adam 2005) and occasionally venture into open water (Burns et al. 2004). Adult female and male crabeater seals can spend from 8 minutes to 15 hours ashore, with juveniles spending more time out of the water (Adam 2005). During the molting season, they form mixed groups, often groups of juveniles, but also groups of males, non-pregnant females, juveniles, and pups (Stirling 1969; Bengtson et al. 2011; Casaux et al. 2011). Weddell seals dive deeper and longer than crabeater seals (91 m for 11.5 min; (Costa et al. 2010)). They tend to congregate in

loose groups along recurrent cracks, leads, and near water access holes in the shore-fast ice habitat (Siniff 1991). The question that arises is whether these differences in phylogenetically related seal species are reflected in ecological differences among their lice.

The present work aims to analyze the population structure of *Antarctophthirus lobodontis* from *Lobodon carcinophaga* (crabeater seals) and *A. carlinii* from *Leptonychotes weddellii* (Weddell seals), in order to compare the reproductive strategies of seal lice in hosts with different behaviors. We propose that the lice have different transmission strategies depending on the diving and foraging behavior of their host. To demonstrate this, we ask whether the probability of bearing lice is related to the developmental stage of the lice (adult or nymph) between the two host species. We then compare the sex ratio of the lice between host species. Finally, we compare the relative abundance of lice between host species in relation to their developmental stage, sex, and species.

Methods

Sample collection

This study was conducted over five austral summers (2014-2015-2016-2019 and 2020) in the Antarctic Specially Protected Area (ASPA) N° 134 (64°09'S, 60°57'W), in the northern sector of the Danco Coast, Antarctic Peninsula (Fig. 2). Lice were collected from the hind flippers of seals (Murray et al. 1965; Thompson et al. 1998; Leonardi 2014) and preserved in 96% ethanol for further analysis. The hind flippers are the preferred site for lice and the abundance represents a reliable proxy for overall burden while reducing host manipulation time (Thompson et al. 1998; Leonardi 2014). Seal (host) handling and immobilization of were approved by the Dirección Nacional del Antártico (Argentina). Sex, weight, and age class were recorded for each host. Once in the laboratory, lice were sexed and classified as adults or nymphs under a stereomicroscope.

Statistical analyses

To model if the probability of a host-bearing lice was related to the developmental stage of the lice (adults or nymphs) between both host species, we used a Binomial GLMM with a logit link function. The logit link function ensures fitted values between 0 and 1, and the Binomial distribution is typically used for probability data. Fixed factors were host species (categorical with two levels) and host developmental stage (categorical with two levels). To incorporate the dependency among observations of the same host, we included the host individual as a random factor. For each host, if a louse was found, it was counted as a success (noted with a 1), otherwise, a 0 was registered when no lice were found on that individual. Hence, this model included both fixed factors with its interaction (host species by developmental stage) and one random factor.

Then, to compare the lice sex ratio between host species, we also used a Binomial GLMM with a logit link function. The fixed factor was the host species (categorical with two levels). To incorporate the dependency among observations of the same host, we included the host individual as a random factor. In this model, the response variable was obtained by counting the number of female lice out of the total number of lice per host.

Finally, to model the relative abundance of lice between host species related to their developmental stage, sex and species we used a Poisson GLMM with a log link function. Fixed factors were host species (categorical with two levels), developmental host stage (categorical with two levels, adult or juvenile), and host sex (categorical with two levels). To incorporate the dependency among observations of the same host, we included the host individual as a random factor. After checking for overdispersion in the Poisson GLMM, we changed to a negative binomial

distribution that can handle overdispersion. Hence, this model included all fixed factors with its interaction (host species by host developmental stage and sex) and one random factor.

All the analyses were done using the R v3.6.3 “Holding the Windssock” software (R. Core Team 2020). The package glmmTMB and nlme were used to fit the models (Brooks et al. 2017; Pinheiro et al. 2021). For testing model assumptions, we used the package DHARMA (Hartig and Lohse 2021). Graphs were done using the package ggplot2 (Wickham 2016). Tukey contrasts were performed with the emmeans function of the package emmeans (Lenth et al. 2020).

Results

Infestation parameters for each species are shown in Table 1a-b; lice sex and classification as adults or nymphs are presented in an additional file [see Additional file 1]’.

Table 1

Infestation parameter (with 95% confidence intervals in parentheses): **a.** *Antarctophthirus lobodontis* from crabeater seals and **b.** *Antarctophthirus carlinii* from Weddell seals, by sex, age class and year.

	Sex		Age class		Year				
	Female (n = 28)	Male (n = 24)	Adult (n = 28)	Juvenile (n = 26)	2014 (n = 10)	2015 (n = 21)	2016 (n = 10)	2019 (n = 10)	2020 (n = 3)
Prevalence (%)	53.6	45.8	14.3	88.5	40.0	33.3	50.0	80.0	100.0
CI 95%	(33.8–72.5)	(25.5–67.2)	(4.0–32.7)	(69.8–97.6)	(15.0–70.9)	(14.6–56.9)	(22.2–77.7)	(44.4–97.5)	(29.2–100)
Mean abundance	129.8	28.29	1.1	168.5	50.40	6.9	11.6	349.3	51.3
CI 95%	(34.4–434.9)	(9.9–85.0)	(0.1–4.6)	(62.1–556.1)	(16.6–120.9)	(2.7–14.3)	(3.1–27.2)	(78.8–110.9)	(22.0–68.3)
Mean Intensity	242.3	61.7	7.5	190.5	126.0	20.7	23.2	436.6	51.3
CI 95%	(82.5–717.6)	(24.3–185.8)	(1.0–18.2)	(72.5–590.5)	(51.0–252.0)	(10.1–31.0)	(7.4–42.4)	(7.5–1326.0)	(22.0–68.3)

Table 1a

Table 1
b

	Sex		Age class		Year				
	Female	Male	Adult	Juvenile	2014	2015	2016	2019	2020
	(n = 24)	(n = 26)	(n = 37)	(n = 17)	(n = 8)	(n = 20)	(n = 10)	(n = 10)	(n = 6)
Prevalence (%)	50.0	50.0	43.6	73.3	75.0	25.0	60.0	50.0	100.0
CI 95%	(28.2–71.8)	(29.9–70.1)	(27.8–60.4)	(44.9–92.2)	(34.9–96.8)	(8.6–49.1)	(26.2–87.8)	(18.7–81.3)	(54.1–100.0)
Mean abundance	3.3	3.3	2.5	4.7	5.7	1.1	3.4	1.3	9.0
CI 95%	(1.64–6.2)	(1.7–6.2)	(1.3–4.7)	(2.6–6.7)	(2.4–12.4)	(0.3–2.5)	(1.5–6.5)	(0.4–2.4)	(4.3–18.2)
Mean Intensity	6.5	6.6	5.7	6.4	7.7	4.4	5.7	2.6	9.0
CI 95%	(4.1–10.7)	(4.1–11.4)	(3.3–10.2)	(4.4–8.5)	(3.8–4.7)	(2.0–6.6)	(3.3–9.7)	(1.6–3.6)	(4.3–18.2)

Regarding the influence of developmental stage of the lice (adults or nymphs) between both host species, we found that, for crabeater seals, the probability of bearing adult lice is marginally higher than having nymphs ($OR_{intraspecies}$ Table 2). For Weddell seals, we found that the probability of bearing adult lice is much higher than having nymphs ($OR_{intraspecies}$, Table 3).

Table 2

Summary of the results of the model for the effect probability of bearing lice was related to the developmental stage of the lice (adults or nymphs) between both Crabeater and Weddell seals. df: Degrees of freedom. LCI and UCI: Lower and upper confidence interval for the estimated probability. $OR_{intraspecies}$ (LCI;UCI): Odds ratio with lower and upper confidence interval for the odds ratio between adult / nymphs lice for each host species. $OR_{interspecies}$ (LCI;UCI): Odds ratio with lower and upper confidence interval for the odds ratio between adult / adult and nymph / nymph lice between host species. It should be noted that if the confidence interval includes 1, the OR is not significant, rendering no difference between groups.

Host species	Lice stage	Probability	Std. error	df	LCI	UCI	p	$OR_{intraspecies}$ (LCI;UCI)	$OR_{interspecies}$ (LCI;UCI)
<i>Crabeater</i>	adult	0.415	0.088	535	0.259	0.591	0.343	adult/nymph: 2.246 (0.967;5.22)	adult/adult: 1.443 (0.58;3.56)
	nymph	0.240	0.063		0.138	0.384	0.001		
<i>Weddell</i>	adult	0.330	0.081		0.193	0.503	0.054	adult/nymph: 4.33 (6.809;73.39)	nymph/nymph: 14.360 (4.73;43.61)
	nymph	0.022	0.010		0.008	0.054	< 0.001		

When comparing adult lice between host species, we found that the probability of bearing adult lice was similar between both host species ($OR_{interspecies}$, Table 2). However, the probability of bearing nymph lice was much higher in crabeater seals compared to Weddell seals ($OR_{interspecies}$, Table 2).

Regarding the sex ratio of lice in each host species, we found that there is a tendency for females in both host species (Table 3). Furthermore, when comparing host species, we found that the probability of having female lice is lower in crabeaters compared to Weddell seals (Table 3).

Table 3

Summary of the results of the model to compare lice sex ratio between Crabeater and Weddell seals. df: Degrees of freedom. LCI and UCI: Lower and upper confidence interval for the estimated probability. OR (LCI;UCI): Odds ratio with lower and upper confidence interval for the odds ratio of female probability between Crabeater / Weddell seal. It should be noted that if the confidence interval includes 1, the OR is not significant, rendering no difference between groups.

<i>Host species</i>	<i>Probability of female</i>	<i>Std. error</i>	<i>df</i>	<i>LCI</i>	<i>UCI</i>	<i>p</i>	<i>OR (LCI;UCI)</i>
<i>Crabeater</i>	0.629	0.027	105	0.574	0.680	< 0.001	0.586 (0.373;0.919)
<i>Weddell</i>	0.743	0.039		0.658	0.813	< 0.001	

Finally, lice abundance was not dependent on sex, so this factor was averaged in the following comparisons. Lice abundance in adult host species was generally low, with the notable result that crabeaters adults bear almost no lice. In juvenile hosts, we found that the abundance of lice in crabeaters was much higher (IC95%: 362.13–2116.00%, Table 4) compared to Weddell seals.

Table 4

Summary of the results of the model to compare relative abundance of lice between Crabeater and Weddell seals related to their developmental stage, sex and species. df: Degrees of freedom. LCI and UCI: Lower and upper confidence interval for the estimated probability. Mean quotient (LCI;UCI): Quotient of mean abundances with lower and upper confidence interval for of the comparison between adults and nymphs between Crabeater / Weddell seals. It should be noted that if the confidence interval includes 1, the mean quotient is not significant, rendering no differences between groups.

<i>Lice stage</i>	<i>Host species</i>	<i>Abundance</i>	<i>Std. error</i>	<i>df</i>	<i>LCI</i>	<i>UCI</i>	<i>p</i>	<i>Mean quotient (LCI;UCI)</i>
<i>Adults</i>	<i>Crabeater</i>	5-0e-06	0.009	500	0.000	inf	0.994	3.80e-05 (0.0;inf)
	<i>Weddell</i>	0.139	0.056		0.063	0	< 0.001	
<i>Nymphs</i>	<i>Crabeater</i>	5.966	2.143		2.946	12.0	< 0.001	10.11 (4.62;22)
	<i>Weddell</i>	0.590	0.252		0.254	1.0	0.218	

Discussion

We analyzed, for the first time, the population structure and reproductive of seal lice strategies under natural conditions in two species of pack-ice seals on the Antarctic Peninsula. Our main conclusion is that *A. lobodontis*, from crabeater seals, and *A. carlinii*, from Weddell seals have different reproductive strategies. Although we did not have information on the reproductive season of crabeater seals, our results confirm that *A. lobodontis* would reproduce at least during the molting season of the seals, whereas the reproduction of *A. carlinii* would occur mainly during the reproductive season of seals (Soto et al. 2022). As we will discuss, these differences may be related to their host's habitat use and foraging behavior.

We found all lice stages (N1, N2, N3, and adults) and potentially viable eggs in crabeater seals. We conducted a preliminary essay on incubated eggs simulating natural conditions (humidity and temperature), and their hatching

was successful under these conditions (Soto, unpublished results). These results could indicate that *A. lobodontis* could reproduce whenever seals haul out during the molting season. The lice would then take advantage of their host's diving behavior, as CS dives shallower and for less time than WS. From the previous study, we know that the mean dive depth of CS was 61 m for 3.8 min (Costa et al. 2010). In summer, they use to dive during darkness and haul out during daylight (see diving details in (Southwell et al. 2012)), probably in response to prey availability (Bengtson and Cameron 2004). Therefore, the combination of short and shallow dives and the continuous haul-out may allow eggs development. This idea is supported by the fact that transmission of *A. lobodontis* should be horizontal, especially between juveniles (Soto et al. 2020). Juveniles spent more time on land than adults. However, this needs to be tested experimentally.

In contrast, only N3 and adults were found in Weddell seals. Accordingly, one of the transmission strategies of *A. carlinii* could be through the mobility of mainly adult lice, which can reproduce and complete a generation in a short period of time. However, as WS dives deeper and longer than CS (91 m for 11.5 min; (Costa et al. 2010)), lice would have less time to reproduce or at least to successfully hatch eggs. As we described in a previous study (Soto et al. 2022), the main way of transmission of *A. carlinii* should be from female seals to their pups. We also observed that adult *A. carlinii* were more likely to be transmitted than nymphs and females more likely than males, the same pattern described for *A. microchir* from sea lions [6].

Seal lice appear to have different reproductive strategies to ensure their reproductive success. For example, *A. microchir* from South American sea lions completes its cycle when the host spends enough time ashore and only newborn pups spend enough time outside of the water (Aznar et al. 2009; Leonardi et al. 2014). In this context, at least during host molting season, *A. lobodontis* probably has more time to complete a generation than *A. carlinii*, depending on the amount of time that its host spends ashore. Such strategies reflect strong co-adaptation and co-evolutionary mechanisms, depending their host life history and behavior.

Regarding the infestation parameters, during the molting season, female crabeater seals reach higher mean abundance and mean intensity than female Weddell seals. Therefore, we assume that *A. lobodontis* is reproducing while the seals are molting. We know from a previous study (Murray et al. 1965) that in Weddell seals dispersion of *A. carlinii* (formerly *A. ogmorhini*) occurs by the transmission of adult lice exclusively from female seals to their pups during the reproductive season, reaching a complete generation in 3–4 weeks. As we did not find any eggs in this sample, we need to elucidate when *A. carlinii* has the opportunity to lay eggs.

When comparing age classes, juveniles of both species had higher prevalence and abundance than adults. From previous studies, we know that these parameters depend mainly on the age class of the hosts (Soto et al. 2020, 2022), with juveniles being more abundant than adults. This pattern may also be related to the diving behavior of the host. Juveniles used to spend less time submerged than adults (Burns et al. 1999) and consequently spend more time on land, which improves lice dispersal.

Recently, a phylogenomic analysis of seal lice showed no divergences between *A. lobodontis*, *A. carlinii*, and *A. ogmorhini* (Leonardi et al. 2019). Some authors postulate that the genetic differences between them are not sufficient to be considered as different species (Dong et al. 2022). However, the differences in the population structure of the two species observed here could indicate that they are different species, or at least that they have undergone different co-evolutionary processes depending on the habit of their hosts.

In conclusion, the study of different seal-lice systems allows us to understand how evolutionary history has shaped the life cycle of each species. Further experimental is needed to fully understand the life cycle of both lice species and to characterize the reproductive strategies they use to ensure their reproductive success.

Abbreviations

CS: crabeater seal; WS: Weddell seal

Declarations

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Availability of data and materials

The data described in this article can be freely and openly accessed as Supplementary material.

Contribution of authors

FAS and MSL wrote the main manuscript text; FAS, MSL, JC, and JN conceived the ideas and designed the methodology; FAS, MSL and JN, collected and processed the samples; FAS and JC analyzed the samples and data; FAS, MSL, JC, and JN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest declaration

The authors declare that they have no competing interests.

Ethical approval

No ethics approval was required for this study

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Figures

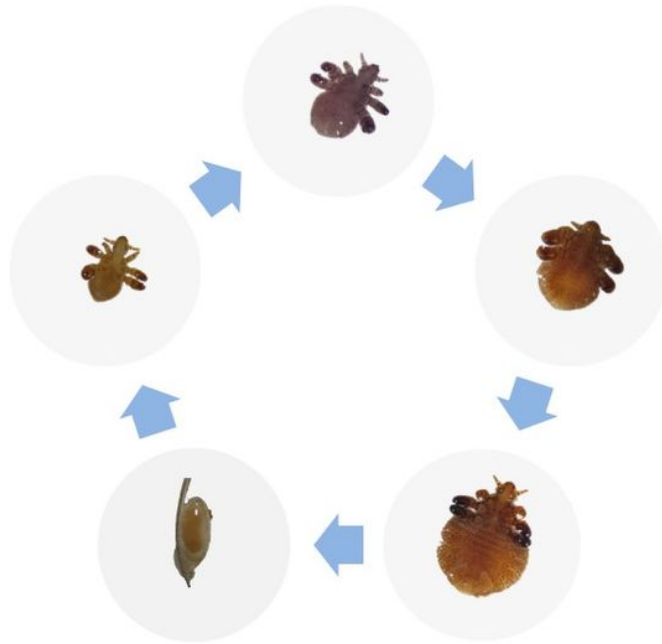


Figure 1

Echinophthiriidae life cycle comprises an egg, three nymphal (N1, N2, N3), and adult (in this figure a female lice).



Figure 2

a General view of Antarctica. **b** Antarctic Specially Protected Area (ASPA) No. 134, in the northern sector of the Danco Coast, Antarctic Peninsula.