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Publication Date
2021-12-01

DOI
10.1016/j.ijppaw.2021.08.005

Peer reviewed
Nasopulmonary mites (Halarachnidae) of coastal Californian pinnipeds: Identity, prevalence, and molecular characterization

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A R T I C L E   I N F O

Keywords:
Halarachne halichoeri
Halarachne mirounga
Orthohalarachne attenuata
Acari
Pinnipedia

A B S T R A C T

Mites from the family Halarachnidae Oudemans 1906 are obligate endoparasites that colonize the respiratory tracts of free-living and captive marine mammals. Infestations can range from mild to severe and result in respiratory tract irritation or impairment. Nasopulmonary acariasis was determined to be a contributing cause of death among several southern sea otters Enhydra lutris nereis Merriam 1904 in a longitudinal study of otter mortality, and proximity to Pacific harbor seals Phoca vitulina richardii Gray 1864 was a significant risk factor for sea otter infestation. Beyond scattered opportunistic reports, each halarachnid mite species’ affinity for particular hosts and the extent of mite transmission between host species is poorly understood. We investigated the identity and prevalence of nasopulmonary mites from Pacific harbor seals, California sea lions Zalophus californianus Lesson 1828, northern elephant seals Miroonga angustirostris Gill 1866, northern fur seals Callorhinus ursinus Linnaeus 1758, and Guadalupe fur seals Arctocephalus philippii townsendi Merriam 1897 to complement published nasopulmonary mite findings from sympatric southern sea otters during a comparable timeframe. Halarachnid mite infestation was common among California sea lions (74.1%), northern fur seals (73.3%), and northern elephant seals (46.6%), but was less common among harbor seals (18.7%) and Guadalupe fur seals (8.8%). Observed host-mite relationships suggest a distinct host specificity, with genus Orthohalarachne infesting otariids, and genus Halarachne infesting phocids and lutrinids along the California coast. Harbor seals and southern sea otters were the primary hosts of H. halichoeri, but one northern elephant seal was infested with both H. mirounga and a single H. halichoeri. We also present the first high-resolution SEM images for H. mirounga and O. attenuata and possible evidence for a new host record for H. halichoeri.

1. Introduction

Mites of the family Halarachnidae Oudemans 1906 are common respiratory parasites of the nose, sinuses, tracheae, bronchi, and lungs of marine mammals that can cause pulmonary irritation and impairment (Dunlap et al., 1976; Baker, 1987; Alonso-Farré et al., 2012). There are two genera Halarachne Allman 1847 and Orthohalarachne Newell 1947 and six described species of halarachnid mites that infest marine mammals: H. americana Banks 1899, H. layanae Furman and Dailey 1980, H. halichoeri Allman 1847, H. mirounga Ferris 1925, O. attenuata Banks 1910, and O. diminuata Doetschman 1944. The genus Orthohalarachne is typically found in otariids and odobenids, while the genus Halarachne is typically found in phocids (Furman and Dailey, 1980). However, each halarachnid mite species’ affinity for particular hosts and the extent of mite transmission between host species is poorly understood. For example, significant risk factors for southern sea otters infested with H. halichoeri include proximity to Pacific harbor seals along with a prior history of captive care and stranding near Moss Landing within Monterey Bay California (Pesapane et al., 2018; Shockling Dent et al., 2019). Although harbor seals were proposed as a source of nasopulmonary mite infestation for southern sea otters, temporally-matched data regarding mite burdens in sympatric harbor

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https://doi.org/10.1016/j.ijppaw.2021.08.005
Received 23 June 2021; Received in revised form 12 August 2021; Accepted 12 August 2021
Available online 14 August 2021
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Characterization of nasopulmonary mite-host associations has been further complicated by repeated revisions to halarachnid mite taxonomy and reclassification of misidentified specimens after the original descriptions of these mites over a century ago (Allman, 1847; Oudemans, 1926; Domrow, 1974; Furman, 1977). Species identification currently requires training on the recognition and interpretation of mite diagnostic features, the use of multiple keys or taxonomic descriptions, and an understanding of revisions to species classification through time, which is impractical for most marine mammal clinicians. This complexity can result in inconclusive or erroneous species determination, and incorrect inferences of host origin (Bush et al., 2021). No contemporary assessment of halarachnid mite species in relation to host marine mammals had been conducted, so it was not known whether existing reports of mite-host associations reflected longstanding host-parasite associations, or merely reflected which mite species dominated at the time or location of individual cases. An empirical study of halarachnid mites across multiple host species that overlap in time and geographic region was needed.

Moribund pinnipeds rescued by The Marine Mammal Center (TMMC; Sausalito, California) that either die in care or require humane euthanasia are routinely necropsied. Parasites are noted whenever observed during necropsy, providing opportunities to study halarachnid mites across multiple host species. We investigated the identity and prevalence of nasopulmonary mites from Pacific harbor seals, California sea lions, northern elephant seals, northern fur seals, and Guadalupe fur seals necropsied by TMMC to complement published nasopulmonary mite findings from southern sea otters that stranded during the same approximate timeframe (Pesapane et al., 2018; Shockling Dent et al., 2019). We also present comparative scanning electron micrographs (SEM) and DNA sequence data for Halarachne mirounga, H. halichoeri, and O. attenuata from different marine mammal hosts.

2. Materials and methods

The response range for TMMC covers approximately 1000 km of the northern and central California coast from Humboldt County to San Luis Obispo County (USA). Moribund pinnipeds are routinely rescued and taken in for triage and rehabilitated and released where possible or necropsied if the outcome is natural death or euthanasia. Occasionally, carcasses are retrieved from beaches for necropsy but generally only those of the endangered Guadalupe fur seal. Nasopulmonary mites were obtained from pinnipeds during necropsy between April 2015 and December 2019 (Table 1). Whole mites were collected from rostral nasal passage, turbinates, and nasopharynx and immediately fixed in 70% ethanol or stored at –20 °C prior to placement in 70% ethanol. Mites were examined by light microscopy to assess morphology and identify genus-specific anatomic features. SEM was also used to facilitate species identification based on published morphological criteria (Oudemans, 1926; Domrow, 1962, 1974; Furman, 1977; Furman and Dailey, 1980). Sample dehydration for SEM was accomplished as previously described (Pesapane et al., 2018).

To develop DNA references for nasopulmonary mite species obtained from different hosts, the 16S genetic region was amplified and sequenced using methods from the parallel study of mites in southern sea otters (Pesapane et al., 2018). Briefly, DNA was extracted using the QiAmp DNA Micro Kit (Qiagen, Valencia, CA) or the PureLink Genomic DNA Mini Kit (Invitrogen, Wallith, MA). A 25-µL volume PCR reaction included GoTaq Green Master Mix (Promega, Madison, WI) and primers with cycling conditions described elsewhere (Black and Piesman, 1994). ExoSAP-IT (ThermoFisher, West Sacramento, CA) was used to purify PCR products prior to sequencing on an ABI 3730 sequencer (Applied DNA Sequencing Facility, Davis, CA; OSU Genomics Shared Resource, Columbus, OH) using the forward and reverse primers. Amplicons were evaluated using CLC Main Workbench bioinformatics software v.7.6.2 (Qiagen, Valencia, CA) and a BLAST search of GenBank (NCBI; http://blast.ncbi.nlm.nih.gov/Blast.cgi).

Nucleotide sequence data reported in this paper are available in the GenBank database under the accession numbers: MZ435787 through MZ435798, and MZ736595. Voucher specimens from each mite species are archived in the acarology collection at The Ohio State University Museum of Biodiversity under accession numbers: OSAL 0150389 (H. mirounga), OSAL 0150392 (H. halichoeri), and OSAL 0150395 (O. attenuata).

To assess the prevalence of nasopharyngeal mite infestations in pinnipeds, the database at TMMC was queried to obtain data that most closely matched those from a prior study of nasopulmonary mite prevalence in southern sea otters (Pesapane et al., 2018). Criteria used to create a composite dataset for each marine mammal host species included: date of death (from January 2016 through December 2019), carcasses that were fresh and never frozen, and a necropsy that included examination of the upper respiratory tract. Criteria for date of death was constrained by the years of data available in the database which began in 2016. Aborted pups or pups that died within 24 h of birth were excluded from analyses. Prevalence and 95% confidence intervals of mite infestation for each host species were calculated using the function prop.test in base R version 3.4.3 (R Core Team, 2017).

Stranding locations were plotted into a geographic information system using ArcMap Pro (ESRI, Redlands, CA, 2021). When GPS coordinates were imprecise, unrealistic, or not recorded, stranding locations were approximated using descriptive data (e.g. “Pacific Grove, Monterey”) and placed at the closest logical beach location. In the few instances where neither geographic coordinates nor descriptive data were reliable, cases were excluded from maps of stranding locations, but were retained for other analyses.

3. Results

3.1. Morphological identification

A total of 398 nasopulmonary mites were obtained for taxonomic identification from harbor seals, California sea lions, northern elephant seals, northern fur seals, and Guadalupe fur seals necropsied between 2015 and 2021 (Table 1). These mites were compared morphologically with mites collected from southern sea otters (Fig. 1E) between 2007 and 2017 in a prior study (Pesapane et al., 2018). All mites from harbor seals exhibited morphological features matching H. halichoeri (see Furman and Dailey, 1980) (Fig. 1D) which include 6 setae (hairs) on the femur of leg III arranged 1–3/1–1, 6 setae on genu of leg IV arranged

Table 1

| Host species | N hosts sampled | Sample timeframe | N mites examined | Mite species |
|--------------|----------------|-----------------|-----------------|-------------|
| HS           | 5              | 2015–2019       | 24              | Halarachne halichoeri |
| NES          | 16             | 2017–2019       | 134             | Halarachne mirounga |
| NF S         | 13             | 2017–2019       | 111             | Orthohalarachne attenuata |
| CSL          | 16             | 2015–2017       | 127             | Orthohalarachne attenuata |
| GFS          | 1              | 2021            | 1               | Orthohalarachne attenuata |
| SSO          | 23             | 2007–2017       | 213             | Halarachne halichoeri |

HS = harbor seals (Phoca vitulina richardi), NES = northern elephant seals (Mirounga angustirostris), CSL = California sea lions (Zalophus californianus), NFS = northern fur seals (Callorhinus ursinus), GFS = Guadalupe fur seals (Arctocephalus philippi townsendii), SSO = southern sea otter (Enhydra lutris nereis).

* Data reproduced from Pesapane et al. (2018).
1–2/0,2/0–1, subcylindrical or saccate opisthosoma (posterior end of the body), and a dorsal shield that is broader posteriorly than anteriorly with linguiform (tongue-shaped) caudal tip. Mites from northern fur seals (Fig. 1A), California sea lions (Fig. 1B), and Guadalupe fur seals (not shown) matched descriptions of *O. attenuata* (see Newell, 1947) with a uniquely long, clavate opisthosoma. Nearly all mites from northern elephant seals were identified as *H. miroungae* (see Furman and Dailey, 1980) (Fig. 1C), however one individual harbored several *H. miroungae* and a single *H. halichoeri*. Distinguishing characteristics of *H. miroungae* include the same setal arrangement as *H. halichoeri* but the dorsal shield is broader anteriorly than posteriorly and the caudal tip tapers to a narrowly rounded point.

### 3.2. Molecular characterization

PCR of individual mites of each species from different host groups yielded amplicons ranging from 380 to 528bp of the 16S region as summarized in Table 2. BLAST results of *H. miroungae* and *H. halichoeri* from this study showed 92–100% homology with *H. halichoeri* sequences previously generated from southern sea otters (Pesapane et al., 2018). BLAST results of *O. attenuata* showed 77–78% homology with a mesostigmatid mite from the superfamily Rhinonyssidae.

### 3.3. Demographic parameters

Among pinnipeds necropsied by TMMC between 2016 and 2019, 1365 matched our case or control selection criteria, with the prevalence of nasopharyngeal infestation ranging from 8.8% in Guadalupe fur seals to 74.1% in northern fur seals (Table 3).

### 3.4. Geographic distribution

*Halarachne halichoeri* infestation was documented as far north as Sea

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**Table 2**

| Mite species          | N | Hosts | Amplicon size | BLAST results (%) homology | GenBank          |
|-----------------------|---|-------|---------------|---------------------------|------------------|
| *Halarachne halichoeri* | 3 | HS    | 380–452      | *H. halichoeri*<sup>a</sup> 96–100% | MZ435787-MZ435789 |
| *Halarachne miroungae* | 3 | NES   | 407–451      | *H. halichoeri*<sup>a</sup> 92–93% | MZ435790-MZ435792 |
| *Orthohalarachne attenuata* | 3 | CSL   | 438–448      | *Ptilonyssus chloris* 77–78% | MZ435793-MZ435795 |
| *Orthohalarachne attenuata* | 3 | NPS   | 426–438      | *Ptilonyssus chloris* 77–78% | MZ435796-MZ435798 |
| *Orthohalarachne attenuata* | 1 | GFS   | 528          | *Ptilonyssus chloris* 77–78% | MZ736595        |

HS = harbor seals (*Phoca vitulina richardi*), NES = northern elephant seals (*Mirounga angustirostris*), CSL = California sea lions (*Zalophus californianus*), NPS = northern fur seals (*Callorhinus ursinus*), GFS = Guadalupe fur seals (*Arctocephalus phillipi townsendii*).

<sup>a</sup> Accession number MH426929 and MH426930 from Pesapane et al. (2018).
Table 3
Nasopharyngeal prevalence of nasopulmonary mites obtained from pinnipeds stranded along the California coast in comparison to pulmonary prevalence in southern sea otters.

| Host species | % Mite prevalence (95% CI) | N hosts | Prevalence timeframe |
|--------------|-----------------------------|---------|----------------------|
| HS           | 18.7 (12.1–27.6)            | 107     | 2016–2019            |
| NES          | 46.6 (38.7–54.6)            | 161     | 2016–2019            |
| NFS          | 74.1 (53.4–88.1)            | 27      | 2016–2019            |
| CSL          | 73.3 (70.5–76.0)            | 1013    | 2016–2019            |
| GFS          | 8.8 (3.3–20)                | 57      | 2016–2019            |
| SSO<sup>a</sup> | 25.6 (19.9–33.4)            | 156     | 2012–2017            |

HS = harbor seals (Phoca vitulina richardi), NES = northern elephant seals (Mirounga angustirostris), CSL = California sea lions (Zalophus californianus), NFS = northern fur seals (Callorhinus ursinus), GFS = Guadalupe fur seals (Arctocephalus philippi townsendi), SSO = southern sea otter (Enhydra lutris nereis).

<sup>a</sup> Data reproduced from Pesapane et al. (2018).

Ranch in Sonoma County (harbor seal; N38.6989, W123.4405) and as far south as China Cove, Monterey County (southern sea otter; N36.50799, W121.94068); a range of nearly 175 linear miles (Fig. 2).

However, infested harbor seals and sea otters in our sample set only overlapped within Monterey Bay, particularly within the highly utilized Elkhorn Slough region (N36.8071, W121.7893). No harbor seals were found to be infested south of Monterey Bay, while no sea otters were found to be infested north of the bay. Other nasopulmonary mite species were found throughout the California coastline from Mendocino County south to Vandenberg State Marine Reserve in Santa Barbara (Fig. 2).

4. Discussion

We investigated the identity and prevalence of nasopulmonary mites infesting Pacific harbor seals, California sea lions, northern elephant seals, northern fur seals, and Guadalupe fur seals to complement published findings from sympatric southern sea otters from the coast of California, USA (Pesapane et al., 2018; Shockling Dent et al., 2019). Although phocids such as harbor seals, grey seals (Halichoerus grypus), hooded seals (Cystophora cristata), spotted seals (Phoca largha), and southern elephant seals (Mirounga leonina) are reported hosts for *H. halichoeri* (Margolis and Dailey, 1972; Furman and Dailey, 1980; Fay and Furman, 1982; Baker, 1987; Alonso-Farré et al., 2012), we present Fig. 2. Spatial distribution of marine mammal stranding sites included in the nasopulmonary mite prevalence dataset. The scale is fixed to allow comparison across hosts. Comparison southern sea otter map produced from dataset in Pesapane et al. (2018).
the first evidence of this mite species infesting a northern elephant seal. To our knowledge, the northern elephant seal harboring both H. halichoeri and H. miroungae also represents the first evidence of co-infection with multiple Halarachne species. Since only one H. halichoeri specimen was recorded from a northern elephant seal, this relationship may represent accidental spillover like that of a captive gentoo penguin (Fain and Mortelmans, 1959; Domrow, 1962). Cross-contamination during collection can be ruled out since no harbor seals were necropsied on the same day as this elephant seal. Although coinfection with O. attenuata and O. diminuta has been reported in other studies (Kim et al., 1980; Gastal et al., 2016), we did not find any O. diminuta among our specimens; this may be attributed to sampling bias for two reasons: first, we only sampled mites from the nasopharynx, and O. diminuta reportedly prefers to parasitize the lungs (Kim et al., 1980; Gastal et al., 2016). However, larvae of both species have been found in the nasopharynx (Fay and Furman, 1982), which is logical since transmission is thought to occur via larval expulsion, followed by invasion of the nares of additional hosts (Kurochkin and Sohobelsky, 1971; Fay and Furman, 1982). Second, nearly all of the Orthohalarachne species from this study were adults; if only larval O. diminuta were present they could have been overlooked. Our results align with the prevailing hypothesis that halarachnid mite genera exhibit distinct host specificity, with Orthohalarachne being restricted to otariids and odobenids (Favel and Procter, 2016) and Halarachne being restricted to phocids and lutrinosids (Furman and Dailey, 1986; Pesapane et al., 2018).

Pacific harbor seals, California sea lions, northern fur seals, and northern elephant seals are the most abundant and widely distributed pinnipeds along the California coast, and their distribution (Kenyon and Wilke, 1953; King, 1983; Gentry, 1998; Burns, John, 2009; Lowry, 2014) overlaps with the southern sea otter range (Tinker et al., 2006). Although Guadalupe fur seals occur in limited numbers in California (Juárez-Ruíz et al., 2018) and their small population has been slow to recover from intense hunting during the 19th century (Starks, Edwin, 1922; Hanni et al., 1997; Aurioles-Gamboa et al., 2010), sightings and strandings have occurred in areas that overlap with southern sea otters (NOAA Office of Ocean Exploration and Research, 2020). Steller sea lions are also relatively uncommon, with small and declining rookeries at Año Nuevo Island and The Farallon Islands in central California (Hastings, 1998; Pitcher et al., 2007). Although southern sea otters range from Half Moon Bay to Point Conception (Tinker et al., 2006), the highest densities of otters occur in central California around the Big Sur coastline and Monterey Bay (U.S. Geological Survey, 2019). A past study revealed that southern sea otters that strand within 1 km of Moss Landing/Elkhorn Slough within Monterey Bay are nearly 5 times more likely to be infested with nasopulmonary mites than sea otters that strand at other coastal locations (Shockling Dent et al., 2019). Southern sea otters and harbor seals commonly interact in this area, but it also serves as a primary release site for rehabilitated otters. Since a history of captive care presents an increased risk of infestation among sea otters (Shockling Dent et al., 2019), it is possible that the release of infested otters in Elkhorn Slough increases the risk of infestation for both sympatric sea otters and harbor seals.

In this study, we obtained contemporaneous nasopulmonary mite samples from all pinniped species that are common near Elkhorn Slough, and may share habitat with mite-infested southern sea otters. The only pinniped species harboring substantial numbers of H. halichoeri were harbor seals, which supports the hypothesis that harbor seals and southern sea otters may be exchanging mites. Despite the lack of samples from Steller sea lions in California in our current sample, Steller sea lions in Alaska were found to be infested with Orthohalarachne (Fay and Furman, 1982) and our results for host specificity among halarachnid mites suggest that it would be extremely unlikely that they would harbor Halarachne spp. Furthermore, Steller sea lions are less likely to spatially overlap with sea otters in Elkhorn Slough.

Amplification of the 16S rDNA region of all three species of nasopulmonary mites from five different host species was successful. The 16S rDNA region of H. halichoeri from harbor seals is nearly identical to that of H. halichoeri collected from southern sea otters (Table 2). This region appears to be highly conserved within H. halichoeri across hosts and geographic regions as H. halichoeri obtained from grey seals in Germany shared 99% homology with mites from southern sea otters (Reckendorf et al., 2019). Halarachne miroungae obtained from northern elephant seals demonstrated high homology with H. halichoeri, which is not unexpected, considering these are closely related, but distinct species. While 16S rDNA sequences of O. attenuata were very similar across samples obtained from California sea lions, Guadalupe fur seals, and northern fur seals, they were very different from H. halichoeri (Table 2). The 16S rDNA region of O. attenuata was generally more homologous to the rhinonyssid mite Pilonysius chloris than Halarachne. Future studies should continue to evaluate the 16S rDNA region as a molecular tool for species identification.

The geographic distribution of infested pinnipeds suggests that H. halichoeri, H. miroungae, and O. attenuata are all present throughout the central California coast. However, mite infestation loads vary among marine mammal species, suggesting that host susceptibility varies. Our sampling data only represents where an animal was found and does not encompass transit or home ranges for those individuals. Some intact points represent animals that stranded far from their normal habitat, and appear to have wandered away from the coastline due to illness or other unknown causes. While our data for stranding location was helpful to identify potential areas of spatial overlap between marine mammals, highlighting possible routes of interspecific mite transmission, they do not encompass all possible host interactions.

Since they were first described in 1847 (Allman, 1847), halarachnid mites have been documented in more than a dozen marine mammal species worldwide (Robiecki et al., 2018), yet few reports include estimates of prevalence (Kenyon et al., 1965; Dunlap et al., 1976; Kim et al., 1980; Fay and Furman, 1982; Baker, 1987; Munro et al., 1992; Dailey et al., 2005; Kuiken et al., 2006; Alonso-Farré et al., 2012; Gastal et al., 2016; Seguel et al, 2018a, 2018b) and our prior study in southern sea otters (Pesapane et al., 2018) is the only study to estimate nasopulmonary mite prevalence in California marine hosts. Our summary data suggests that nasopulmonary mite infestation is the norm among California sea lions (74.1%), northern fur seals (73.3%), and northern elephant seals (46.6%), while infestation is less common among harbor seals (18.7%) and Guadalupe fur seals (8.8%) (Table 3). Prior studies of northern fur seals in the Pribilof Islands of Alaska report a 100% prevalence of nasopulmonary mite infestation (Dunlap et al., 1976; Kim et al., 1980), and prior studies of harbor seals in Alaska and Scotland report 75% and 9.5% prevalence, respectively (Fay and Furman, 1982; Munro et al., 1992). No reports of mite prevalence are available for elephant seals or sea lions, but prevalence among a small sample of Galápagos sea lions (Zalophus wollebaeki) was 16.7% (Dailey et al., 2005). Although nasopulmonary mites have not previously been reported in Guadalupe fur seals, in South American fur seals (Arctocephalus australis) the reported prevalence varies from 9.4% in Peru (Seguel et al., 2018a), to 68.2% in Brazil (Gastal et al., 2016), and 100% in Chile (Seguel et al., 2018b). Our values likely underestimate the true prevalence of nasopulmonary mite infestation in each host population because examination of the respiratory tract was limited to the nasopharynx in some cases, and because mites may be difficult to detect during necropsy (Pesapane et al., 2018).

The taxonomy of halarachnid mites has been subjected to numerous revisions, and some species identification of mites obtained from marine mammal hosts have been controversial, particularly within the genus Halarachne. Species within this genus are morphologically very similar, with only slight differences in the shape of certain attributes such as the dorsal shield or opisthosoma, and the presence or absence of setae. Relative comparisons of shapes like “more saccate” or “more subcylindrical” are difficult because they are based on verbal descriptions or hand drawings; as a result, species identification is best achieved via direct morphological comparison with fully characterized type
specimens. Presence-absence assessments are even more challenging, especially if the specimen quantity is poor, e.g. because the absence of setae may simply represent sample artifact. High-resolution images like the SEM images generated in this study are advantageous because they facilitate direct comparison and allow for better evaluation of subtle characteristics.

We have generated the first high-resolution SEM images for *H. mirounga* and *O. attenuata*, reported nasopulmonary mite infestation in Guadalupe fur seals, and presented possible evidence for a new host record for *H. halichoeri* and coinfection of a marine mammal with multiple *Halarachne* species. Aside from one northern elephant seal, we found that harbor seals are the only other marine mammal species examined that was infested with *H. halichoeri* during the same timeframe as the southern sea otter study, supporting prior hypotheses of parasite exchange among these two populations (Pesapane et al., 2018; Shockling Dent et al., 2019). Nasopulmonary mite infestation appears to be common in marine mammals from the California coast. Heavy mite infestations can be pathogenic to both pinnipeds and lundrith hosts (Dunlap et al., 1976; Baker, 1987; Alonso-Farr et al., 2012; Shockling Dent et al., 2019), and parasite loads of as few as 20 mites appear to be capable of causing pathology in affected animals (Pay and Furman, 1982). These mites could potentially harbor and transmit bacterial or viral pathogens between animals. Because captive care and animal translocation activities have the potential to amplify mite loads and facilitate spread of mites and their associated microbiota, treatment with acaricides should be considered for animals in care and prior to local release or translocation.

**Declaration of competing interest**

None.

**Acknowledgements**

Field support was provided by the rescue and response team of The Marine Mammal Center. Archibald was supported by the Morris Animal Foundation Veterinary Student Scholar program (D20ZO-608). The authors appreciate the technical support provided by Patricia Kysar, C.E. Foundation Veterinary Student Scholar program (D20ZO-608). The *´Alonso-Farr Allman, G.J., 1847. No. IV. Description of a new genus and species of tracheary translocation.*

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