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Original Article

Nasal mites in seabirds and shorebirds: the role of host morphology and phylogeny on measures of parasitism

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ABSTRACT

Parasitic mites have evolved to live in the nasal airways of their hosts and have been reported in many seabirds and shorebirds worldwide. However, patterns of mite occurrence and the relationship with morphological and phylogenetic characteristics of hosts are still poorly understood. Here we present data from 1011 seabirds and shorebirds, representing 68 species across seven orders and 16 families. We dissected and measured the morphology of the nasal cavity to investigate parasitism patterns, recognizing this structure as a habitat for mites. We also classified birds phylogenetically, through bill morphometry, examining whether these features are associated with parasitological indices. In total, we describe 372 host–parasite associations across 25 avian taxa, reporting 11 new association records, including undescribed mite species. Our results suggest that bill morphology, influenced by the phylogeny of hosts, affects parasitic indices. Although the dimensions of the nasal opening were not related to the prevalence of infected hosts, we observed a positive influence on the mean rates of parasite intensity and abundance, and mites were lacking in species with vestigial or absent nostrils. Our study provides insights into the habitat and diversity of nasal mites, serving as a baseline for future ecological and evolutionary studies on host–parasite interactions.

Keywords: Acari; bill morphology; Charadriiformes; Ereynetidae; Gaviiformes; parasitological indices; Podicipediformes; Procellariiformes; Rhinonyssidae; Turbinoptidae

INTRODUCTION

Seabirds and shorebirds harbour a wide variety of parasites, including helminths, protozoa, and arthropods. Mites (Arachnida: Acari) are one of the most diverse and frequent parasites associated with birds, with at least 3000 described species (Proctor and Owens 2000). Among the parasitic mites, five families of acariform (Ereynetidae, Turbinoptidae, and Cytoditidae) and parasitiform (Melicharidae and Rhinonyssidae) mites have evolved independently to live in the nasal passages or lungs of birds (Knee and Galloway 2017). Nasal mites have been surveyed in birds worldwide, including Australia (Domrow 1969), Canada (Knee and Galloway 2017), Japan (Kadosaka *et al.* 1987), Russia (De Rojas *et al.* 2020, Dimov 2020a,b), South Africa (Gretillat 1961, Vanstreels *et al.* 2019), United States (Pence 1975, Spicer 1987), and Brazil (Mascarenhas *et al.* 2022, Gastal *et al.* 2022, 2023), among other localities.

Rhinonyssidae (Mesostigmata), the most diverse group of nasal mites, holds over 510 known species, parasitizing almost all presently recognized orders of seabirds and shorebirds (Beron 2020, Dimov 2020a, Hilario-Pérez and Dowling 2020). These mites are slow-moving haematophagous endoparasites that occur primarily in the nasal cavity in association with the nasal turbinates, scrolls of highly vascularized epithelial tissue, and occasionally in the tracheal tissues, lungs, and body cavities (Porter and Strandtmann 1952, Bell 1996). Ereynetidae (Prostigmata) are tissue-feeding nasal mites found throughout the nasal cavity of aquatic birds, such as Anseriformes, Charadriiformes, and Pelecaniformes (Fain 1956, Domrow 1965, Knee *et al.* 2008). Turbinoptidae

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(Astigmata) are also tissue-feeding mites that dwell in the superficial cutaneous regions of the nasal cavity, feeding on corneous layers of the skin of Charadriiformes and Coraciiformes (Fain 1994, Knee *et al.* 2008, Mascarenhas and Müller 2021). Cytoditidae (Astigmata) is a small family of exudate-feeding parasites that occur throughout the nasal cavity and the sinus walls, lungs, and air sacs of Coraciiformes (Fain 1994, Mascarenhas and Müller 2021). The apparent host restrictions and limited diversity of respiratory mites reported in birds more broadly may be due to insufficient sampling and research rather than reflecting true patterns of host specificity or distribution. In this sense, differences in nasal cavities of bird hosts would contain characteristics, including shelter and food, potentially influencing infection rates as well as survival of mites. This host–parasite dynamics aligns with a theory known as the Red Queen hypothesis (Van Valen 1973), which suggests that biotic interactions, such as host resistance and parasite adaptation, are more important in evolutionary and coevolutionary processes than abiotic conditions (Van Valen 1973, Brockhurst *et al.* 2014).

Nasal mites share a key evolutionary novelty among mites, i.e. extreme body miniaturization, which allows them to exploit many niches unsuitable for most other arthropods (Dabert 2005). Body characteristics such as reduced shielding and reduced setation, combined with reduced mobility, restrict nasal mites to the respiratory system of their hosts, which explains why they are not found in bird nests, like other parasites (Hilario-Pérez and Dowling 2018). In addition, as there are no food resources for these parasites outside their host (i.e. blood and tissues), it is assumed that nasal mites avoid leaving their hosts, as this would decrease their survival (Dimov 2020a). Therefore, due to this range restriction and habitat specificity, little is known about the biology and means of transmission of nasal mites between hosts.

The primary hypothesis is that nasal mites transmit from parents to chicks during food provisioning (Murray 1966), as this involves bill-to-bill contact. Another hypothesis is that birds transmit nasal mites during group socialization, such as preening and courtship, including courtship feeding (Amerson 1967). Therefore, the bill of birds can be considered the gateway to these parasites, and the nasal cavity is their habitat. In this sense, morphological characteristics of nasal structures probably influence mite presence and transmission.

Nasal mites have vast possibilities of habitats to explore, as birds have a wide diversity of bill shapes, structures, and sizes, which are associated with foraging techniques, olfactory mechanisms, and temperature regulation (Luther and Greenberg 2014). This morphological bill diversity leads to different types of nostrils and internal structures of the nasal cavity (Huxley 1867). On birds, the nasal cavity is divided by the median septum and connected to the oropharynx through the choana (King 1986, Dyce *et al.* 2010), a natural cavity reminiscent of the keratinization of the palatine process rather than its fusion during embryological development (Ferguson 1988). Inside the bill, respiratory turbinates are highly convoluted, and often scrolled, structures lined with a moist mucociliate epithelium (Bang 1961, 1971). Although morphologically diverse, the turbinates lack insulation and contain vascularized tissues (Luther and Greenberg 2014). These characteristics make them favourable habitats, especially for haematophagous mites. The organization of the bone trabeculae also varies among species, coinciding with the bill variation related to the feeding habits of birds (Genbrugge *et al.* 2012).

Seabirds and shorebirds are important but overlooked components of coastal marine ecosystems. They link marine and terrestrial environments on a global scale, contributing significantly to interhabitat connectivity, nutrient cycling, and the provision of multiple ecosystem services (Signa *et al.* 2021, Gaiotto *et al.* 2022). They generally live in dense aggregations in breeding, feeding, roosting, and resting areas, and are capable of exploring several areas during a single day (Bugoni and Vooren 2005). Some species can be resident in a single area, while others make long migrations from breeding to wintering grounds (Frankish *et al.* 2020, Brown *et al.* 2021). In this sense, mites can reside for months in a given breeding area but migrate thousands of kilometres with their host towards wintering areas, under the same habitat and conditions.

In this study, we examined nasal mites in different species of seabirds and shorebirds from Brazil and southwestern USA, aiming to quantify parasitism rates, and compare bill and nasal cavity structures of hosts, with parasitological indices. In addition, we summarized the biodiversity of avian nasal mites in seabirds and shorebirds and reported on any novel host–parasite associations. We hypothesize that variation in nostril morphology and internal structures of the bill, which are related to the foraging habits of birds, as well as their phylogenetic relationships, will influence the presence of nasal mites. We predict that the prevalence of infection will be higher in birds with larger nostrils, as they serve as gateways for mites, in comparison to birds with less complex or absent nostrils. Moreover, we expect an elevated mean intensity of infection in birds with more tissue area and/or richly vascularized and fewer bone trabeculae, as this will favour the presence of nasal mites. Finally, we expect that parasitological indices can provide clues to understanding the host–parasite interactions and association between nasal mite transmission among different groups of seabirds and shorebirds.

MATERIAL AND METHODS

Sampling and identification of birds and mites

We sampled seabird and shorebird carcasses found stranded on beaches or available in rehabilitation centres along the coasts of Rio Grande do Sul, Santa Catarina, São Paulo, and Rio de Janeiro states, in Brazil, in addition to California (USA), between 2015 and 2022. Only animals found dead during routine beach surveys or that died under care in rehabilitation centres were considered for this study. We only necropsied carcasses with an estimated time of death within the last 24 h. The carcasses were then taken to a local laboratory where they were frozen for later necropsies.

For extraction of nasal mites from birds, we dissected the nasal cavities of the hosts during necropsy using pruning pliers and scissors. To facilitate visualization, we either cut the nasal cavity sagittally (Amaral and Rebouças 1974) or transversely (Gastal *et al.* 2022), depending on the size of the bird and the hardness of the bill, and examined the cavities with a stereomicroscope (Olympus® SZ51). Any mites observed were collected with a brush (number 0) and stored in 70% ethanol for later examination. Following visual inspection, the nasal cavities were flushed with room temperature water and filtered with a 150-μm mesh sieve. The resulting filtrate was examined using a stereomicroscope at 10–100× magnification. Mites were collected with a brush (number 0) and stored in 70% ethanol. For microscopic analysis, we cleared the specimens in lactophenol or Nesbitt's solution and slide-mounted them in Hoyer's medium (Krantz and Walter 2009).

We identified mites to the family, genus, or species level using identification keys (Pence 1975, Knee and Proctor 2006, 2010) and species description from the primary bibliography (Knee 2008, Dimov 2013, 2020b, Dimov and Spicer 2013, Knee 2018, Gastal *et al.* 2022, 2023). Voucher specimens were deposited at the *Coleção Acarológica do Instituto Butantan* (IBSP), São Paulo, Brazil, while birds collected in Brazil were deposited at the *Coleção de Aves da Universidade Federal do Rio Grande*—FURG (CAFURG), a collection part of the Subtropical Biodiversity Center (CBS-FURG), Rio Grande, Brazil.

Data presented for *Ardenna gravis* (O'Reilly, 1818), *Calonectris borealis* (Cory, 1881), and *Puffinus puffinus* (Brünnich, 1764) are an addition to the analysed individuals in Gastal *et al.* (2022) and for *Spheniscus magellanicus* (Forster, 1781) an addition to the examined individuals published by Gastal *et al.* (2018). For *Daption capense* (Linnaeus, 1758) we considered the number of individuals published by Gastal *et al.* (2023), but here we explore the interaction of parasitological indices with morphological traits of hosts.

Host morphological trait analysis

For anatomical comparison, we grouped birds according to the type of nostril: slit-like, tubular, nearly closed or vestigial, and absent (Schreiber and Burger 2001, Zusi and Livezey 2006) (Fig. 1). As morphometric traits, we measured culmen length, height at the basis of the bill, and choana total length, and length and

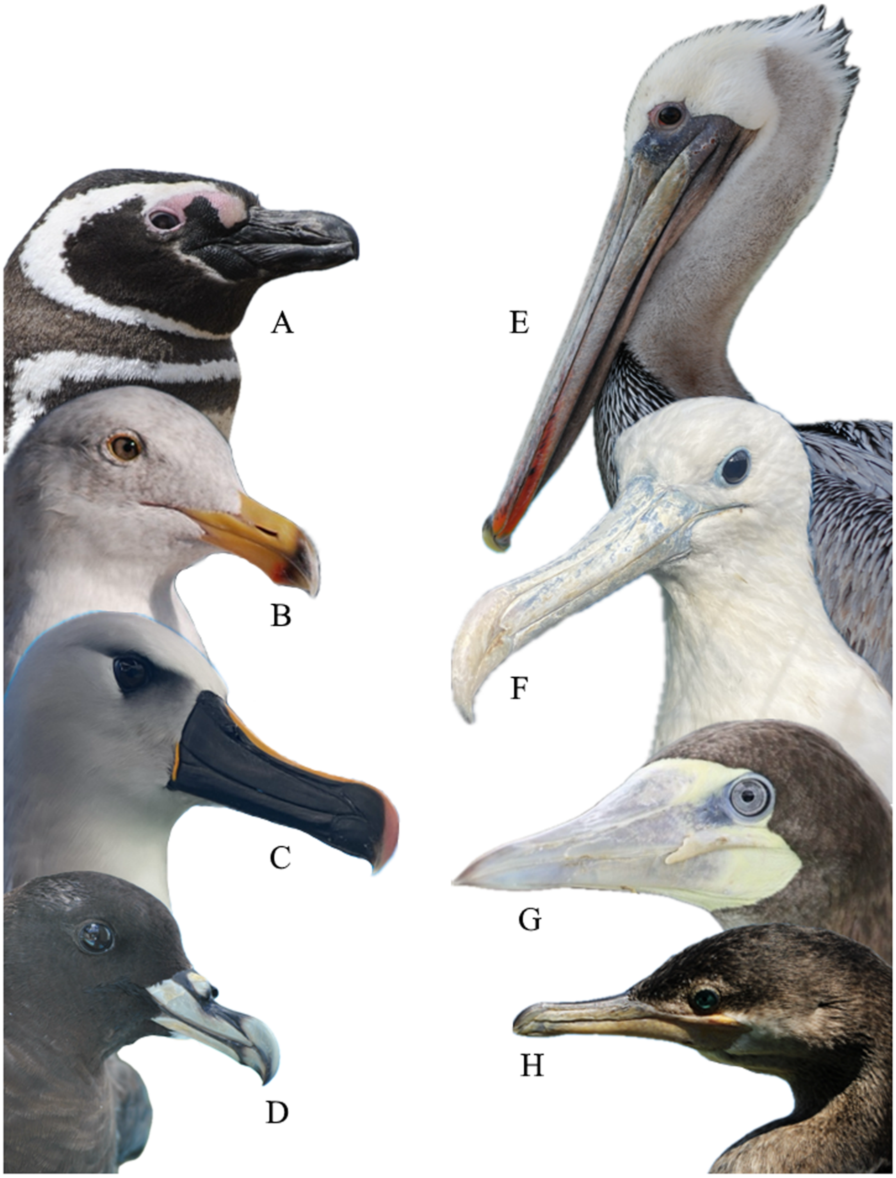

Figure 1. Examples of seabird and shorebird nostril types. Slit-like nostrils: A, *Spheniscus magellanicus* (Sphenisciformes); B, *Larus californicus* (Charadriiformes). Tubular nostrils: C, *Thalassarche chlororhynchos* (Procellariiformes); D, *Procellaria aequinoctialis* (Procellariiformes). Nearly closed: E, *Pelecanus occidentalis* (Pelecaniformes); F, *Fregata magnificens* (Suliformes). Absent: G, *Sula leucogaster* (Suliformes); H, *Nannopterum brasilianum* (Suliformes).

width at the largest portion of the choana for all bird species. We also measured nostril height and width for birds with slit-like and tubular nostrils. In addition to the dissections and morphometric measurements, we photographed the nasal cavity to make an internal structural comparison between the taxa analysed. We then separated the nasal cavity for each species by macroscopic visualization, considering the predominance of connective tissue and vascularized respiratory epithelium (50% or more covered by epithelial tissue), or predominance of bone trabeculae (50% or more of the cavity extension).

Parasitological indices and data analysis

We estimated the parasitological indices of prevalence (P%), mean intensity (MI), and mean abundance (MA), according to Bush *et al.* (1997), calculated for bird orders, families, and species. We then compared the indices per parasitized host (P%, MI, and MA>0) according to the families using permutational multivariate analysis of variance (PERMANOVA), with a Bray–Curtis dissimilarity index (Anderson 2001, 2017), using the package *vegan* v.2.6-4 (Oksanen *et al.* 2022). To investigate the interaction between hosts' morphological traits and parasitological indices for parasitized and nonparasitized hosts (P%, MI, and MA≥0), we used a Bayesian phylogenetic mixed model, using the package *brms* v.2.22.0 (Bürkner 2017).

To investigate possible correlations between morphometric traits before selecting parameters for the Bayesian models, we performed a Spearman correlation test through a correlation matrix using the *Hmisc* v.5.2-3 package (Harrel-Jr 2024), as morphometric traits were nonparametric. To evaluate the patterns and relationship between the morphometric traits, we then performed a principal component analysis (PCA), using the packages *FactoMineR* v.2.11 (Lê *et al.* 2008) and *factoextra* v.1.0.7 (Kassambara and Mundt 2020). To select correlated morphometric traits and group them for the Bayesian models, we adopted the following criteria: (i) portion of the bill measured (external, i.e. nostril width, nostril height, culmen, and height at the basis of the bill; or internal, i.e. choana total length, choana length at the larger portion, and choana width at the larger portion); (ii) ecological reasoning to group traits, aiming to represent an entrance to and a habitat for the mites; (iii) contribution of each variable to the main dimensions of the PCA; and (iv) direction and proximity of the traits within dimensions on the PCA. We then reduced the morphometric parameters to four traits: culmen length, nostril height, choana total length, and choana width at the largest portion. From those, we calculated a ratio between culmen length and choana length (Eq. 1) and nostril height and choana width at the largest portion (Eq. 2), which resulted in the parameters 'Culmen vs. Choana' and 'Nostril vs. Choana', implemented in our Bayesian models. To evaluate correlations between nostril and cavity types, we performed a chi-square test and, subsequently, a multiple correspondence analysis (MCA), using the same PCA packages. We then grouped the morphological characteristics of the bill into six bill types (Supporting Information Table S1) to be implemented as the 'bill type' parameter in the Bayesian models.

$$\text{Culmen vs. Choana} = \frac{\text{Choana length} \times 100}{\text{Culmen length}} \qquad (1)$$

where 'Culmen vs. Choana' is the ratio between the mean of the choana total length and the mean of culmen length measured by bird species.

$$\text{Nostril vs. Choana} = \frac{\text{Choana width} \times 100}{\text{Nostril height}} \qquad (2)$$

where 'Nostril vs. Choana' is the ratio between the mean of the choana width at the largest portion and the mean nostril height measured by bird species.

We also investigated if the morphometric traits had any phylogenetic signal before selecting mixed effects models. For that, we generated 1000 phylogenetic trees by submitting a list of all bird species for which we had morphometric traits measured to BirdTree.org (Jetz *et al.* 2012). To generate our trees, we used Hackett *et al.* (2008) as a source tree, a set of 10000 trees with 9993 operational taxonomic units (OTUs) each. We then selected the best tree, based on total branch length, mean tree length across all trees, and range (minimum and maximum) of tree lengths using the *ape* v.5.8-1 (Paradis and Schliep 2019) and *phytools* v.2.4-4 (Revell 2024) packages. To investigate if there is a phylogenetic signal in morphometric traits and whether their evolution follows Brownian motion (Felsenstein 1985), we calculated the phylogenetic signal lambda (λ; Pagel 1999).

For our Bayesian phylogenetic mixed models, we transformed mite prevalence (P%) in proportion (0.00–1.00) and used mean abundance and mean intensity raw values. We used hurdle-gamma distributions and log link, selected through a distribution analysis using the *fitdistrplus* package v.1.1-11 (Delignette-Muller and Dutang 2015). Our parameters were 'Culmen vs. Choana', 'Nostril vs. Choana', and bill type, with species as a fixed effect. We defined our intercept prior as normal (0, 10), and our coefficient priors as normal (0, 5), class 'b' (Bürkner 2017). We set our final models to run 8000 iterations, with 3000 as warm up, using four chains, adjusting the sampling behaviour (adapt_delta = 0.999), and the depth of the phylogenetic tree evaluated in each interaction (max_treedepth = 20), defined after a few trials to obtain a final model with no divergent transitions after warm up and reduction factor for all parameters at convergence equal to 1 (Rhat = 1; Bürkner 2017).

For the graphical representations of raw data of each index, we used *ggplot2* v.3.4.4 (Wickham 2016), *viridis* v.0.6.4 (Garnier *et al.* 2023), and *hrbrthemes* v.0.8.0 (Rudis *et al.* 2020). For visualization of the principal coordinates analysis, from the dissimilarity matrix, we used the package *vegan* v.2.6-4 (Oksanen *et al.* 2022). All statistical analysis and graphical representations of indices and statistical models were generated in R software v.4.4.3 (R Core Team 2025) using the cited packages.

RESULTS

Parasitological indices of nasal mites

We examined a total of 1011 birds from seven orders, 16 families, 40 genera, and 68 species (Table 1). Taking all birds examined, the overall prevalence of nasal mites was 36.8%, the mean intensity was 10.3, and the mean abundance was 3.8 mites per host. Among birds sampled in Brazil, 18.9% had nasal mites, the mean intensity of infection was 18.9, and the mean abundance was 3.6 mites per

Table 1. Prevalence (P%), mean intensity (MI), and mean abundance (MA) of nasal mites in different orders and families of hosts and the number of genera, species, infected birds, and collected mites.

Order/family	No. of genera examined	No. of species examined	No. of birds sampled	No. of infected birds	No. of collected mites	P%	MI	MA
Charadriiformes	**16**	**28**	**351**	**91**	**2911**	**25.9**	**32.0**	**8.3**
Charadriidae	2	2	5	1	1	20.0	1.0	0.2
Haematopodidae	1	1	1	0	0	0	0	0
Laridae	8	14	315	87	2885	27.6	33.2	9.2
Recurvirostridae	1	1	7	3	8	42.9	2.7	1.1
Scolopacidae	3	5	15	1	18	6.7	18	1.2
Stercorariidae	1	5	8	0	0	0	0	0
Gaviiformes	**1**	**2**	**3**	**1**	**18**	**33.3**	**18**	**6.0**
Gaviidae	1	2	3	1	18	33.3	18	6.0
Pelecaniformes	**1**	**2**	**2**	**0**	**0**	0	0	0
Pelecanidae	1	2	2	0	0	0	0	0
Podicipediformes	**5**	**6**	**24**	**3**	**4**	**12.5**	**1.3**	**0.2**
Podicipedidae	5	6	24	3	4	12.5	1.3	0.2
Procellariiformes	**12**	**23**	**277**	**49**	**365**	**17.7**	**7.4**	**1.3**
Diomedeidae	3	4	45	0	0	0	0	0
Oceanitidae	1	1	4	0	0	0	0	0
Procellariidae	8	17	228	54	400	23.7	7.4	1.8
Sphenisciformes	**1**	**1**	**244**	**39**	**532**	16.0	13.6	2.2
Spheniscidae	1	1	244	39	532	16.0	13.6	2.2
Suliformes	**4**	**7**	**110**	**0**	**0**	**0**	**0**	**0**
Fregatidae	1	1	21	0	0	0	0	0
Phalacrocoracidae	2	4	28	0	0	0	0	0
Sulidae	1	2	61	0	0	0	0	0
TOTAL	**40**	**68**	**1011**	**372**	**3830**	**37**	**10.3**	**3.8**

host. The prevalence of nasal mites in birds sampled in the USA was 37.5%, with mean intensity of 63.1 and mean abundance of 23.7 mites per host.

Among the mite families, Rhinonyssidae had the highest prevalence (18.3%), with mean intensity of 20.6 and mean abundance of 3.8 mites per host. Ereynetidae had a prevalence of infection of 1%, mean intensity of 6.4, and a mean abundance of 0.1 mites per host. Finally, Turbinoptidae had the lowest prevalence (0.9%) and mean abundance (0.5 mites per host), but the highest mean intensity (59.9 mites per host) of the three families of mites found in seabirds and shorebirds in this study.

The species-rich Charadriiformes (gulls, skuas, terns, plovers, and sandpipers) was the order holding most samples (34.7%), with 351 individuals and 28 bird species. Of these, 25.9% of the birds sampled were parasitized by nasal mites. The prevalence of mites parasitizing Laridae was 27.6%, with mean intensity of 33.2 and a mean abundance of 9.2 mites per host.

Procellariiformes (albatrosses and petrels) represented 27.4% of the hosts examined, with a prevalence of 17.7%. Among the three families of Procellariiformes examined, we only found mites in Procellariidae hosts (P% = 23.7, MI = 7.4, and MA = 1.8 mites per host).

Penguins (Sphenisciformes), comprising only Spheniscidae, represented 24.1% of the birds examined, with mite parasitism P% = 16, MI = 13.6, and MA = 2.2 mites per host.

A small number of individuals of Podicipediformes (grebes), Gaviiformes (loons), and Pelecaniformes (pelicans and herons) were sampled, together representing only 2.9% of the birds. Podicipediformes, which includes only the Podicipedidae, had a parasitism P% = 12.5, MI = 1.3, and MA = 0.2 mites per host. For Gaviiformes, represented by Gaviidae loons, mite parasitism P% was 33.3, MI = 18, and MA = 6 mites per host. We did not find nasal mites in pelicans (Pelecanidae), the only family of Pelecaniformes analysed in this study. We also did not find nasal mites in either of the three Suliformes families analysed (boobies, cormorants, and frigatebirds), despite a relatively large sample size (*n* = 110, 10.9% of bird samples). Overall, data for parasitism prevalence, mean intensity and mean abundance (Fig. 2) varied widely across host families, from 9.1 to 100% for prevalence, 0.1 to 103.7 for mean abundance, and 1 to 145.2 mites per host for mean intensity.

The list of analysed taxa containing the number of parasitized and nonparasitized individuals and parasitological P%, MA, and MI per mite family and/or species, as well as host sampling location and previous records of nasal mites for the analysed hosts are shown in Table 2. Among Charadriiformes, kelp gull (*Larus dominicanus* Lichtenstein, 1823) was the most sampled taxon, comprising 48.7% of individuals. For this species, the nasal mite *Larinyssus* sp. was observed in 32.8% of the birds, with MA = 13 and MI = 39.8 mites per host. Other gull species, sampled in lower numbers, were also parasitized by nasal mites. We also identified the first record of *Turbinoptes strandtmanni* Boyd, 1949 in brown-hooded gulls [*Chroicocephalus maculipennis* (Lichtenstein, 1823)]. Co-infections (more than one species of mite parasitizing the nasal cavity of a host) were observed only for North American birds, such as California gull (*Larus californicus* Lawrence, 1854), which

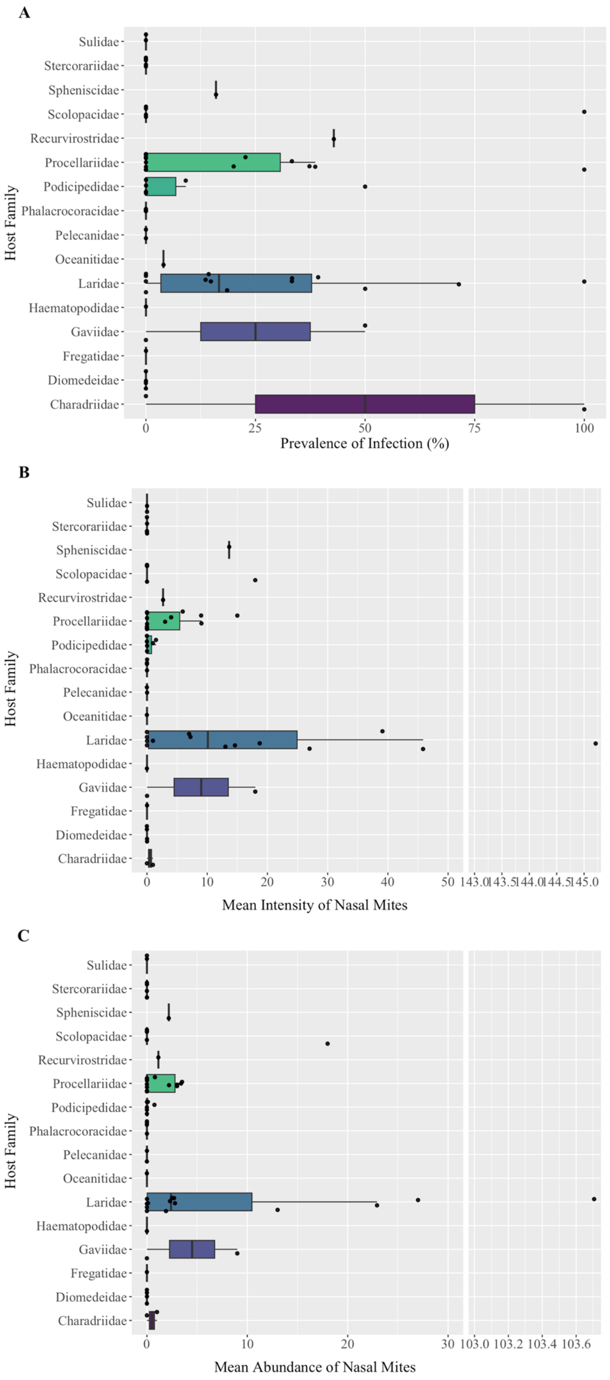

Figure 2. Distribution analysis of parasitism by nasal mites in seabirds and shorebirds from Brazil and western USA presented by bird family. A, prevalence data; B, mean intensity data; C, mean abundance data.

was parasitized by *Sternostoma boydi* Strandtmann, 1951 and *Turbinoptes* sp., and Western gull (*Larus occidentalis* Audubon, 1839), parasitized by *Larinyssus* sp. and *Sternostoma* sp. Among other Charadriiformes species, the first records of nasal mites for the white-backed stilt (*Himantopus melanurus* Vieillot, 1817), parasitized by *Rhinonyssus himantopus* Strandtmann, 1951, and the snowy-crowned tern (*Sterna trudeaui* Audubon, 1838), parasitized by *Larinyssus* sp., are noteworthy. We recorded for the first time the occurrence of *Rhinonyssus pluvialis* Fain & Johnston, 1966 parasitizing semipalmated plovers (*Charadrius semipalmatus* Bonaparte, 1825) and *Sternostoma boydi* parasitizing royal tern [*Thalasseus maximus* (Boddaert, 1783)].

For Procellariiformes, Manx shearwater (*Puffinus puffinus*) was the most sampled species (24.1%), with parasitism P% = 37.3, MA = 2.2, and MI = 5.9 mites per host. Here we also present the first record of Ereynetidae in Procellariiformes, parasitizing spectacled petrels (*Procellaria conspicillata* Gould, 1844) and Cory's shearwaters (*Calonectris borealis*). We highlight the occurrence of co-infection between mites of Ereynetidae and *Rhinonyssus borealis* Gastal, Mascarenhas and Bugoni, 2022, in shearwaters as hosts. We found a new species of *Rhinonyssus* (unpubl. data) parasitizing the Southern fulmar [*Fulmarus glacialoides* (Smith, 1840)], of which a high-quality description was not obtained due to the small number of mites (*n* = 4) and limited quality of specimens prepared on slides. We found no nasal mites in larger Procellariiformes (*n* = 67) including albatrosses *Diomedea* spp. and *Thalassarche* spp. (Diomedeidae), and giant-petrels *Macronectes* spp. (Procellariidae). For Sphenisciformes, we only sampled the Magellanic penguin (*Spheniscus magellanicus*). From those, 39 (16%) out of 244 were parasitized by *Rhinonyssus sphenisci* Fain and Mortelmans, 1959, with mean abundance of 2.2 and mean intensity of 13.6 mites per host.

We present here the first record of Turbinoptidae mites from Gaviiformes. Of the two species analysed, the common loon [*Gavia immer* (Brünnich, 1764)], was parasitized by Turbinoptidae mites (MA = 9, MI = 18 mites per host). For Podicipediformes, we present the first record of *Rhinonyssus alberti* Strandtmann, 1956 in white-tufted grebe [*Rollandia rolland* (Quoy & Gaimard, 1824)]. Of the six species of Podicipediformes sampled, two specimens (50%) of white-tufted grebe were parasitized. The mean abundance for this host was 0.7 and mean intensity was 1.5 mites per host.

Morphological traits of hosts

Among birds examined, 61.5% (*n* = 622) had slit-like nostrils, including 25 species of Charadriiformes, two species of Gaviiformes, six species of Podicipediformes, and one species of Sphenisciformes. We observed tubular nostrils in 27.4% (*n* = 277) of birds, of which 21 species are Procellariiformes. Only one species belonging to Suliformes (*n* = 21) and two Pelecaniformes species (*n* = 2) had the nearly closed nostril type (2.2%). The Suliformes species (*n* = 89; 8.8% of birds sampled) had no nostril (i.e. nostril absent).

Internally, we determined the nasal cavity of 84.4% of the birds examined (*n* = 853, from 55 species) as having a predominance of connective tissue and vascularized respiratory epithelium (Fig. 3A–C), and 15.6% of birds (*n* = 158, 14 species) with predominance of bony trabeculae in the internal cavity (Fig. 3D–F).

The length of the choana in relation to the culmen of the birds was less than 25% in 72 individuals from six species. This measure varied between 26 and 50% in 188 birds of 17 species and was greater than 50% in 740 individuals of 35 species. Examples of variation in the ratio of choana length to culmen are shown in Figure 4.

Table 2. Host records for nasal mites (Rhinonyssidae, Turbinoptidae, and Ereynetidae) collected from seabirds and shorebirds in Brazil (BR) and United States (USA), including prevalence (P%), mean intensity (MI), mean abundance (MA), host collection locality, and previous records for the hosts.

Bird order/family/species	Examined birds	P%	MA	MI	Mite family or species	Host collection locality	Mite species previously recorded for the host
Charadriiformes							
Charadriidae							
Charadrius semipalmatus	1	100	1	1	*Rhinonyssus pluvialis*	Rio Grande, Rio Grande do Sul, BR	*Rhinonyssus coniventris* [1,2] **This study**
Pluvialis dominica	4	0	0	0		Rio Grande, Rio Grande do Sul, BR	*Rhinonyssus pluvialis*[3]
Haematopodidae							
Haematopus palliatus	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Laridae							
Anous stolidus	1	0	0	0		Offshore area, Rio de Janeiro, BR	No records found
Chroicocephalus maculipennis	27	18.5	2.7	14.6	*Turbinoptes strandtmanni*	Rio Grande, Rio Grande do Sul, BR	**This study**
Gygis alba	1	0				Ilha da Trindade, Espírito Santo, BR	No records found
Larus argentatus	1	100	27.0	27.0	*Sternostoma boydi*	Los Angeles, California, USA	*Larinyssus orbicularis* [4,5,6] *Sternostoma boydi* [1] *Turbinoptes strandtmanni* **This study** [1]
Larus californicus	7	28.6	16.7	58.5	*Sternostoma boydi*	Los Angeles, California, USA	*Sternostoma boydi* [7]
	7	42.9	86.9	202.7	*Turbinoptes strandtmanni*		*Turbinoptes strandtmanni* [7;8] **This study**
Larus dominicanus	171	32.8	13.0	39.8	*Larinyssus* sp.	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Larinyssus orbicularis* [9,10] **This study**
Larus occidentalis	14	42.9	14.7	34.3	*Larinyssus* sp.	Los Angeles, California, USA	*Sternostoma boydi* [7]
	14	21.4	8.2	38.3	*Sternostoma boydi*		**This study**
Phaetusa simplex	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Rynchops niger	5	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Larinyssus orbicularis*[11]
Sterna hirundinacea	27	14.8	1.9	13.0	*Larinyssus* sp.	Rio Grande, Rio Grande do Sul, BR São Sebastião, São Paulo, BR	*Larinyssus orbicularis* [12] **This study**
Sterna hirundo	22	13.6	2.5	18.7	*Larinyssus* sp.	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Larinyssus orbicularis* [1,5] *Larinyssus iohanssenae* [6,13] *Sternostoma boydi* [1,12] **This study**
Sterna trudeaui	7	14.3	0.1	1.0	*Larinyssus* sp.	Florianópolis, Santa Catarina, BR	**This study**
Thalasseus acuflavidus	28	39.3	2.8	7.2	*Larinyssus* sp.	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR São Sebastião, São Paulo, BR	*Larinyssus orbicularis* [12] *Sternostoma boydi* [12] **This study**
Thalasseus maximus	3	33.3	2.3	7.0	*Sternostoma boydi*	Rio Grande, Rio Grande do Sul, BR	*Larinyssus orbicularis* [4] **This study**
Recurvirostridae							
Himantopus melanurus	7	42.9	1.1	2.7	*Rhinonyssus himantopus*	Rio Grande, Rio Grande do Sul, BR	**This study**

(Continued)

Table 2. (Continued)

Bird order/family/species	Examined birds	P%	MA	MI	Mite family or species	Host collection locality	Mite species previously recorded for the host
Scolopacidae							
Calidris alba	10	0	0	0		Rio Grande, Rio Grande do Sul, BR Quissamã, Rio de Janeiro, BR	*Sternostoma boydi* [14] *Rhinonyssus coniventris* [1,15]
Calidris canutus	2	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Rhinonyssus coniventris*[15]
Calidris fuscicollis	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Numenius hudsonicus	1	0	0	0		Los Angeles, California, USA	No records found
Phalaropus lobatus	1	100	18.0	18.0	*Sternostoma boydi*	Los Angeles, California, USA	*Sternostoma boydi* [16] **This study**
Stercorariidae							
Stercorarius antarcticus	1	0	0	0		Macaé, Rio de Janeiro, BR	No records found
Stercorarius chilensis	4	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found
Stercorarius longicaudis	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Stercorarius parasiticus	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Stercorarius skua	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Gaviiformes							
Gaviidae							
Gavia immer	2	50.0	9.0	18.0	Turbinoptidae	Los Angeles, California, USA	**This study**
Gavia stellata	1	0	0	0		Los Angeles, California, USA	No records found
Pelecaniformes							
Pelecanidae							
Pelecanus erythrorhynchos	1	0	0	0		Los Angeles, California, USA	No records found
Pelecanus occidentalis	1	0	0	0		Los Angeles, California, USA	No records found
Podicipediformes							
Podicipedidae							
Aechmophorus clarkii	2	0	0	0		Los Angeles, California, USA	No records found
Aechmophorus occidentalis	11	9.1	0.1	1.0	*Sternostoma boydi*	Los Angeles, California, USA	**This study**
Podicephorus major	5	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Podiceps nigricollis	1	0	0	0		Los Angeles, California, USA	*Rhinonyssus alberti*[17]
Podilymbus podiceps	1	0	0	0		Los Angeles, California, USA	*Rhinonyssus podilymbi* [1,5] *Neoboydaia colymbiformi* [1]
Rollandia rolland	4	50.0	0.75	1.5	*Rhinonyssus alberti*	Rio Grande, Rio Grande do Sul, BR	**This study**
Procellariiformes							
Diomedeidae							
Diomedea exulans	2	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Phoebetria fusca	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Thalassarche chlororhynchos	19	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found
Thalassarche melanophris	23	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found

Oceanitidae							
Oceanites oceanicus	4	0	0	0		Florianópolis, Santa Catarina, BR Offshore area, Rio de Janeiro, BR	No records found
Procellariidae							
Ardenna gravis	22	22.7	3.4	15.0	*Rhinonyssus procellaricus*	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Rhinonyssus procellaricus* [18] **This study**
Ardenna grisea	3	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found
Calonectris borealis	44	31.8	2.6	8.2	*Rhinonyssus borealis*	Rio Grande, Rio Grande do Sul, BR	*Rhinonyssus borealis* [18] **This study**
Calonectris borealis	44	15.9	0.9	5.6	Ereynetidae	Rio Grande, Rio Grande do Sul, BR	**This study**
Calonectris sp.	14	21.4	0.4	2.0	*Rhinonyssus borealis*	Florianópolis, Santa Catarina, BR	**This study**
Calonectris sp.	14	14.3	0.8	5.5	Ereynetidae	Florianópolis, Santa Catarina, BR	**This study**
Calonectris diomedea	5	0	0	0		Florianópolis, Santa Catarina, BR	No records found
Calonectris edwardsii	1	0	0	0		Florianópolis, Santa Catarina, BR	No records found
Daption capense	3	33.3	3.0	9.0	*Rhinonyssus nenecoi*	Rio Grande, Rio Grande do Sul, BR	*Rhinonyssus nenecoi*[19]
Fulmarus glacialis	1	0	0	0		Los Angeles, California, USA	No records found
Fulmarus glacialoides	5	20.0	0.8	4.0	*Rhinonyssus* sp. nov. 1	Florianópolis, Santa Catarina, BR	**This study**
Macronectes giganteus	16	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Macronectes halli	7	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Procellaria aequinoctialis	30	0	0	0		Florianópolis, Santa Catarina, BR	No records found
Procellaria conspicillata	1	100	3.0	3.0	Ereynetidae	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	**This study**
Pterodroma brevirostris	1	0	0	0		Rio Grande, Rio Grande do Sul, BR	No records found
Pterodroma incerta	2	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found
Pterodroma mollis	6	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	No records found
Puffinus puffinus	67	37.3	2.2	5.9	*Rhinonyssus procellaricus*	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR Praia Grande, São Paulo, BR Araruama, Cabo Frio and Quissamã, Rio de Janeiro, BR	*Rhinonyssus procellaricus* [18] **This study**
Sphenisciformes							
Spheniscidae							
Spheniscus magellanicus	244	16.0	2.2	13.6	*Rhinonyssus sphenisci*	Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR	*Rhinonyssus sphenisci* [20] **This study**
Suliformes							
Fregatidae							
Fregata magnificens	21	0	0	0		Florianópolis, Santa Catarina, BR Praia Grande, São Paulo, BR	No records found

(Continued)

Table 2. (Continued)

Bird order/family/species	Examined birds	P%	MA	MI	Mite family or species	Host collection locality	Mite species previously recorded for the host
Phalacrocoracidae							
Nannopterum brasilianum	25	0	0	0		Rio Grande, Rio Grande do Sul, BR Florianópolis, Santa Catarina, BR Praia Grande, São Paulo, BR	No records found
Phalacrocorax pelagicus	1	0	0	0		Los Angeles, California, USA	No records found
Phalacrocorax penicillatus	1	0	0	0		Los Angeles, California, USA	No records found
Phalacrocorax urile	1	0	0	0		Los Angeles, California, USA	No records found
Sulidae							
Sula dactylatra	2	0	0	0		Offshore area, Rio de Janeiro, BR	No records found
Sula leucogaster	59	0	0	0		Florianópolis, Santa Catarina, BR Praia Grande, São Paulo, BR Arraial do Cabo, Rio das Ostras, and Quissamã, Rio de Janeiro, BR	No records found

[1] Pence (1973).
[2] Amaral and Rebouças (1974).
[3] Fain and Johnston (1966).
[4] Strandtmann (1948).
[5] Pence (1972).
[6] De Rojas *et al.* (2020).
[7] Spicer (1978).
[8] Knee *et al.* (2008).
[9] Zumpt and Patterson (1951).
[10] Zumpt and Till (1955).
[11] Pence (1975).
[12] Silva *et al.* (2018).
[13] Dimov (2013).
[14] Strandtmann (1951).
[15] Knee and Proctor (2010).
[16] Fain (1963).
[17] Strandtmann (1956).
[18] Gastal *et al.* (2022).
[19] Gastal *et al.* (2023).
[20] Gastal *et al.* (2018).

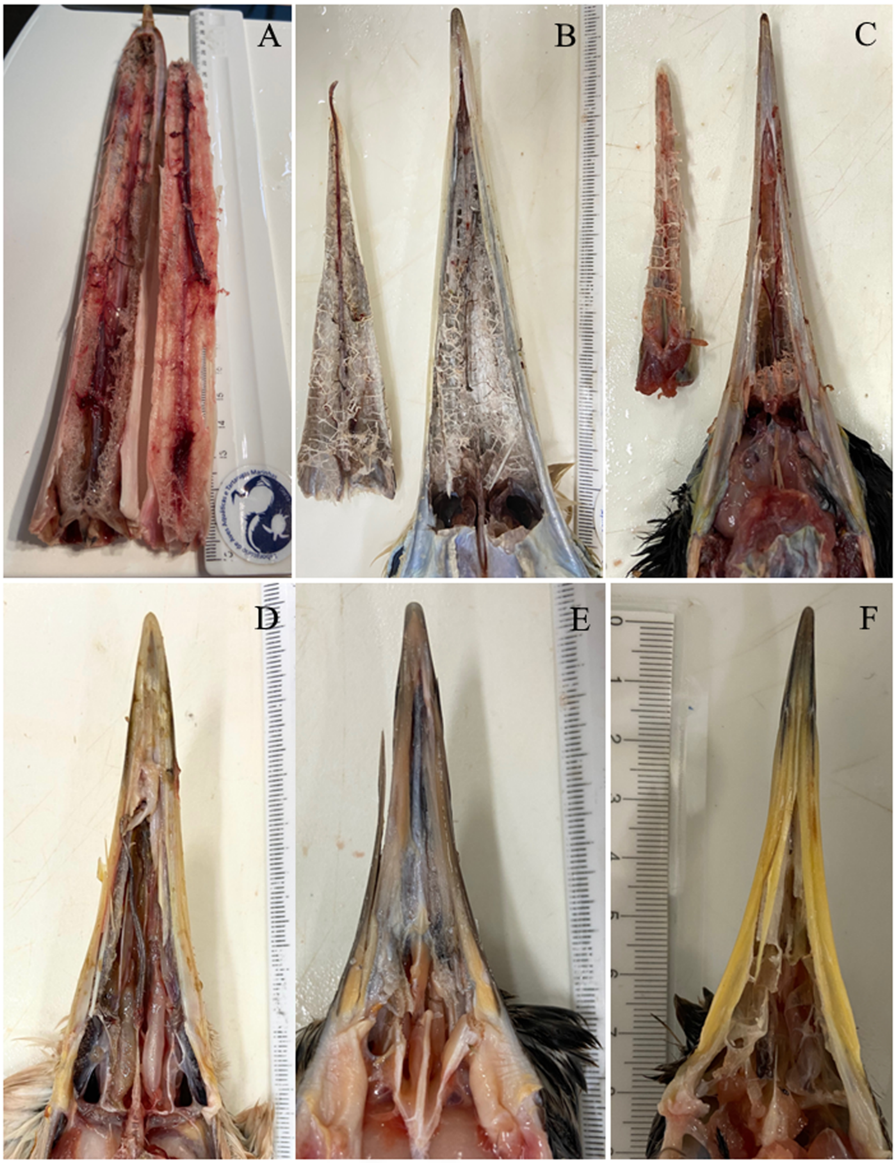

Figure 3. Examples of nasal cavity of seabirds and shorebirds. Predominance of connective tissue and vascularized respiratory epithelium: A, *Pelecanus erythrorhynchos*; B, *Fregata magnificens*; C, *Sula leucogaster*. Predominance of bony trabeculae: D, *Larus dominicanus*; E, *Spheniscus magellanicus*; F, *Calonectris borealis*.

Statistical models

We detected eight principal coordinates from the dissimilarity matrix of parasitism prevalence, 12 from the mean intensity and 14 from the mean abundance. The variance explained by the two principal coordinates for each index is given in Supporting Information Table S2. Procellariidae, Recurvirostridae, Laridae, and Gaviidae have similar variance for the prevalence of hosts infected by mites (Fig. 5A). Charadriidae and Podicipedidae have a similar variance for mean intensity of mites, as well as Laridae, Scolopacidae, and Spheniscidae (Fig. 5B). This grouping pattern was statistically supported by the PERMANOVA ($F = 2.55$, $R^2 = .576$, $P = 0.007$), demonstrating a significant effect of host family on mite intensity. On the other hand, the variance of mean abundance leads to other groupings: Charadriidae with Recurvirostridae, and Spheniscidae with Laridae and Procellariidae (Fig. 5C) We did not observe a pattern of prevalence in different host families (Fig. 5A). The principal coordinates did not influence the variance of mean intensity values in Gaviidae (Fig. 5B) nor the prevalence of Charadriidae (Fig. 5A).

Morphometric traits were strongly correlated (Supporting Information Table S3) for different bird species ($P < 0.01$). To achieve more meaningful and interpretable results, we then performed a PCA to select and group correlated traits, reducing the parameters for the statistical models. We obtained a percentage of variability of 35.4% in dimension 1, which had as major contributor height at the bill basis ($\text{ctr} = 31.289$, $\cos^2 = 0.776$), followed by culmen ($\text{ctr} = 22.381$, $\cos^2 = 0.555$), and choana total length ($\text{ctr} = 16.702$, $\cos^2 = 0.414$). Dimension 2 had a percentage of

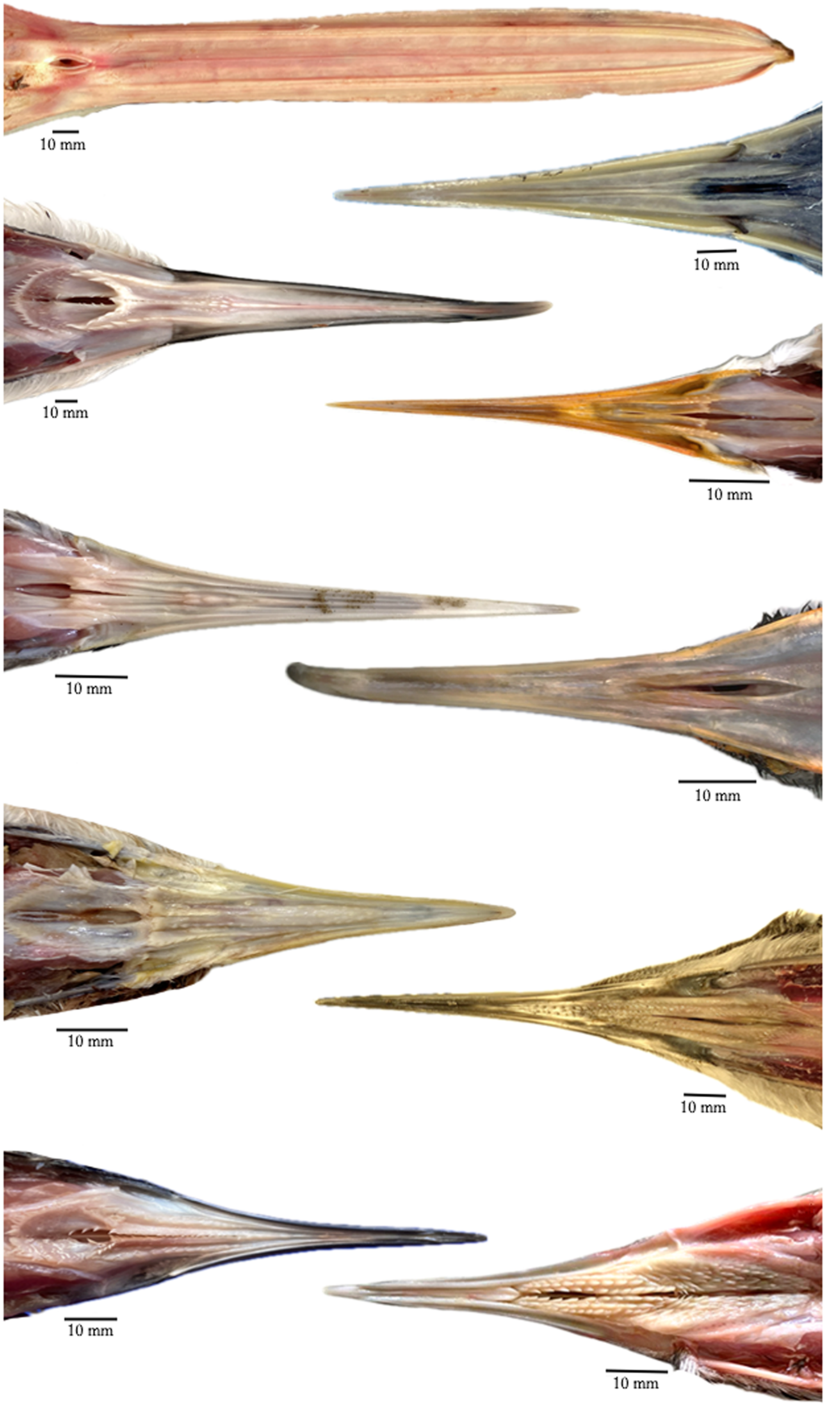

Figure 4. Choana length relative to culmen examples, showing the difference between choana sizes. A, *Pelecanus erythrorhynchos* (5.7%); B, *Sula dactylatra*; C, *Thalassarche chlororhynchos* (35.1%); D, *Thalasseus acuflavidus* (39.1%); E, *Podicephorus major* (31.6%); F, *Nannopterum brasilianum* (32.1%); G, *Larus dominicanus* (64.5%); H, *Gavia immer* (63.5%); I, *Puffinus puffinus* (68.4%); J, *Spheniscus magellanicus* (80.6%).

variability of 20.9%, with major contributions from nostril height (ctr = 37.299, $\cos^2 = 0.545$), followed by choana length at the largest portion (ctr = 34.004, $\cos^2 = 0.497$), and choana width (ctr = 13.984, $\cos^2 = 0.204$). Based on the contributions of each variable, we then accounted for the direction of each variable and proximity from each other within the PCA (Fig. S1) to select and reduce the morphometric traits. Finally, our Bayesian models incorporated two morphometric parameters, 'Culmen vs. Choana', representing culmen length and total choana length, and 'Nostril vs. Choana', representing nostril height and choana width. The morphological characteristics of the bill analysed were also strongly correlated ($P < 0.01$). In our MCA, we obtained a percentage of variability of

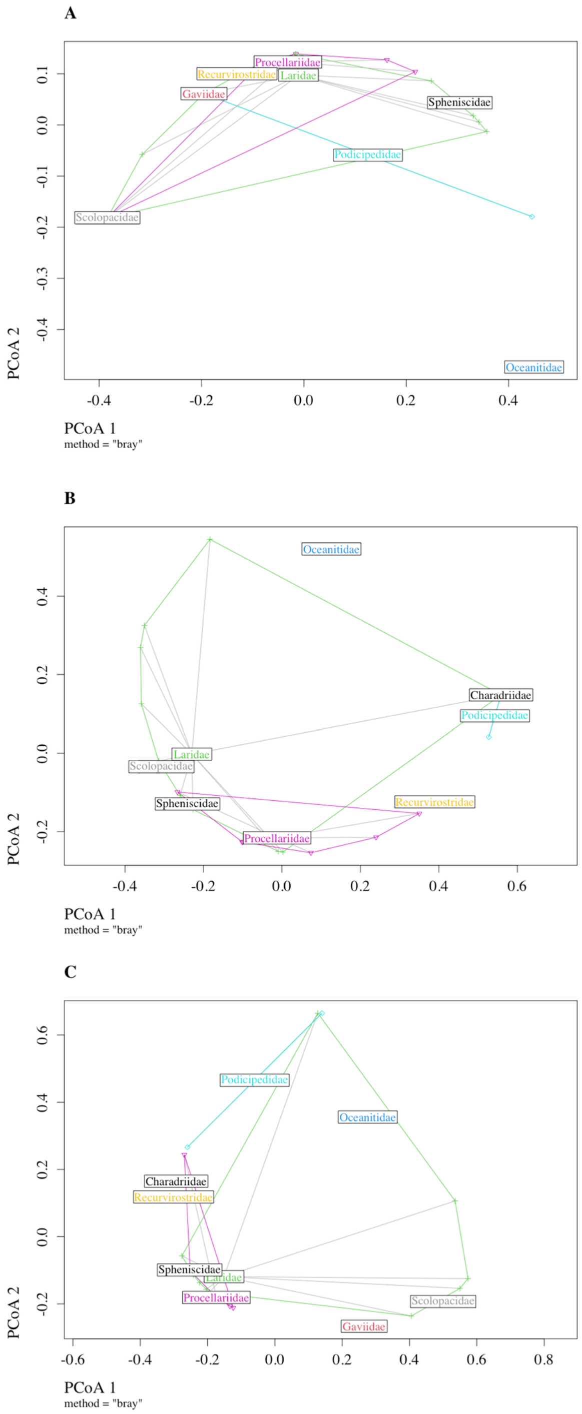

Figure 5. Principal coordinates of the dissimilarity matrix of parasitological rates of nafal mites in different host families of shorebird and seabird from Brazil and USA. A, prevalence data; B, mean intensity data; C, mean abundance data.

54.7% in dimension 1, which had as major contributors of the internal structures of the nasal cavity predominance of bone trabeculae (ctr = 42.235, $\cos^2 = 0.820$), followed by predominance of connective tissue (ctr = 7.765, $\cos^2 = 0.820$), and type of nostril absent (ctr = 35.788, $\cos^2 = 0.660$). Dimension 2 had a percentage of variability of 33.3% in dimension 2, with major contributions from tubular nostril (ctr = 68.462, $\cos^2 = 0.943$), followed by slit-like nostril (ctr = 14.094, $\cos^2 = 0.367$), and absent nostril (ctr = 17.444, $\cos^2 = 0.196$). Internal structures of nasal cavity had no contribution to dimension 2. We then adopted the same approach as for the morphometric traits, observing the distribution and proximity from each other within the MCA graph (Fig. S2). As morphological traits did not seem to follow a specific pattern, we then grouped all bill characteristics into a single parameter 'bill type', which resulted in six different bill types (Table S1), to be used in the Bayesian models.

The best tree among the 1000 phylogenetic reconstructions was 885 (Supporting Information Fig. S3), with a total branch length of 1284.3 units. Lengths across all trees ranged from 1284.3 to 1821.7 units, with a mean of 1495.1 units. We then used tree 885 to calculate the phylogenetic signal for 'Culmen vs. Choana' ($\lambda = 1.007$), 'Nostril vs. Choana' ($\lambda = 1.008$), and 'Culmen vs. Choana' + 'Nostril vs. Choana' ($\lambda = 1.008$), which supported a phylogenetic signal consistent with Brownian motion.

Finally, when relating morphological bill traits from hosts to parasitological indices of nasal mites, we found a credible interval (CI) and positive effect of 'Culmen vs. Choana' on the mean intensity (lower 95% CI = 0.01, upper 95% CI = 0.07), and a weaker effect of 'Nostril vs. Choana' (lower 95% CI = 0.00, upper 95% CI = 0.04; Table 3). On the other hand, mean abundance of nasal mites had a credible positive effect of 'Nostril vs. Choana' (lower 95% CI = 0.01, upper 95% CI = 0.06), with a weaker and positive effect of 'Culmen vs. Choana' (lower 95% CI = 0.00, upper 95% CI = 0.08; Table 3). 'Nostril vs. Choana' also had a weak positive effect on the prevalence of nasal mites in seabirds and shorebirds (lower 95% CI = 0.00, upper 95% CI = 0.03; Table 3). Bill type had no effects in any of the parasitological indices.

DISCUSSION

Overall, the prevalence of mites found in this study (36.8%) was higher than that reported in previous studies on avian nasal mites. In Taiwan, the prevalence of nasal mites in birds was 19% (Maa and Kuo 1965), while in the USA it was 16% based on 1927 birds (Pence 1973), and 17% based on 502 individuals (Spicer 1987). Similarly, in Canada, Knee *et al.* (2008) found 16.2% prevalence, and De Rojas *et al.* (2020) reported 4.4% prevalence in birds from Russia. However, if we analysed birds sampled in Brazil ($n = 963$) separately from those sampled in the USA ($n = 48$), the prevalence in Brazil was similar to values worldwide (18.9%). The prevalence on birds sampled in California was higher (33.3%) when compared to the number of hosts from Brazil and elsewhere but based on fewer samples analysed. This high prevalence may be due to the species composition of the sample, since *Larus* spp. made up most of the hosts (45.8%, $n = 22$). In contrast, samples from other countries were analysed across a broader range of orders and species. Notwithstanding, the present review and previous studies show that a substantial proportion of birds host nasal mites, regardless of where they are sampled or the habitats occupied by hosts. However, our study demonstrated that phylogenetic classification of hosts may influence parasitism indices in birds by affecting bill morphology, which in turn shapes the available habitat for nasal mites.

Table 3. Coefficients from the Bayesian phylogenetic mixed model explaining the effects of morphological predictors on prevalence, mean intensity, and mean abundance of mites parasitizing seabirds and shorebirds.

	Estimate	Est. error	Lower 95% CI	Upper 95% CI	Bulk_ESS	Tail_ESS
Prevalence						
Intercept	−4.74	3.89	−12.43	2.86	13025	14097
Culmen vs. Choana	0.04	0.02	0.00	0.08	8895	10275
Nostril vs. Choana	0.03	0.01	0.01	0.06	12591	14217
bill_type2	0.02	5.01	−9.74	9.84	31483	14169
bill_type3	0.01	5.05	−10.00	9.79	33276	13527
bill_type4	−0.52	3.56	−7.45	6.48	11962	13971
bill_type5	−0.07	5.00	−9.86	9.74	32592	15023
bill_type6	0.64	3.58	−6.29	7.67	12490	13699
Mean intensity						
Intercept	−2.45	3.80	−9.88	4.93	13005	14173
Culmen vs. Choana	**0.04**	**0.01**	**0.01**	**0.07**	**14844**	**12953**
Nostril vs. Choana	0.02	0.01	0.00	0.04	21641	14822
bill_type2	−0.04	5.01	−9.89	9.85	34372	14616
bill_type3	−0.05	5.12	−10.01	10.02	34909	14853
bill_type4	−0.19	3.61	−7.29	6.80	12557	13954
bill_type5	−0.03	5.00	−9.87	9.81	29969	14502
bill_type6	0.31	3.63	−6.81	7.45	12569	13195
Mean abundance						
Intercept	−4.74	3.89	−12.43	2.86	13025	14097
Culmen vs. Choana	0.04	0.02	0.00	0.08	8895	10275
Nostril vs. Choana	**0.03**	**0.01**	**0.01**	**0.06**	**12591**	**14217**
bill_type2	0.02	5.01	−9.74	9.84	31483	14169
bill_type3	0.01	5.05	−10.00	9.79	33276	13527
bill_type4	−0.52	3.56	−7.45	6.48	11962	13971
bill_type5	−0.07	5.00	−9.86	9.74	32592	15023
bill_type6	0.64	3.58	−6.29	7.67	12490	13699

The intercept corresponds to bill_type1 (absent nostrils with prevalence of bone trabeculae as internal bill structure; Supporting Information Table S1), and mean values for 'Culmen vs. Choana' and 'Nostril vs. Choana', in relation to which all other categories are compared. Bulk_ESS and Tail_ESS represent the effect sample size measures. Lower 95% CI, the lower credible interval with 95% of credibility; Upper 95% CI, the upper credible interval. The potential scale reduction factor for all parameters at convergence is one (Rhat = 1). Significant positive effects are indicated in bold type.

It is well known that the phylogenetic history of an organism can be an important determinant of recent traits (Lauder 1982). Therefore, we suggest that host evolution may shape the ability of parasites to infect hosts. This arms race (the Red Queen hypothesis) suggests that the dynamics of host–parasites has an important role in coevolutionary processes (Van Valen 1973, Brockhurst *et al.* 2014), as observed in other seabirds (Hammer *et al.* 2010). In this sense, due to the specificity of some nasal mites, it is possible that the parasites constantly adapt to new traits of a host, or even to new phylogenetically related hosts in a co-evolutionary process. Host–parasite specificity in nasal mites and birds is generally at the host family level and sometimes at the genus level. Therefore, to unravel the coevolutionary dynamics of nasal mites with seabirds and shorebirds, temporal studies in parasitism indices are needed, accounting for different hosts and their phylogenetic relationships.

There are over 700 described species of avian nasal mites worldwide (Beron 2020, 2022), and Ereynetidae, Turbinoptidae, and Cytoditidae are much less diverse and less frequently reported than Rhinonyssidae (Hilario-Pérez and Dowling 2018). In this study, we collected ereynetids, turbinoptids, and rhinonyssids, while the Cytoditidae have not been reported from Brazil to date. As seen in similar studies (Pence 1973, Spicer 1987, Knee *et al.* 2008), rhinonyssids were the most common nasal mites found. *Rhinonyssus* was the most common genus of nasal mites in waterbirds investigated in our study, with eight mite species recovered from 95 hosts belonging to 11 bird species, suggesting high adaptability to different host species and nasal cavity morphologies.

Ereynetid mites were reported by Pence (1975) as parasitizing Podicipediformes. These mites are rare and, when present, occur in small numbers (Knee and Galloway 2017). In this study, we report for the first time the occurrence of Ereynetidae mites in two species of Procellariiformes, belonging to a new species (S.B. Gastal unpubl. data), therefore demanding further investigation.

Turbinoptids were less frequent but, when found, often occurred in high numbers (up to 128 mites on a single host) (Knee *et al.* 2008). *Turbinoptes strandtmanni* is the only species known to parasitize Charadriiformes. In North America, turbinoptids occur in several species of gulls and terns, as well as in shorebird species (Pence 1973). In our study, we documented the occurrence of *T. strandtmanni* in California gull, confirming a previous report by Spicer (1978), and the presence of turbinoptid mites for the first time in Gaviiformes, but further research is necessary toward mite species identification.

In Brazil there is a single record of Turbinoptidae, *Congocoptes brasiliensis* Fain & Aitken 1970, parasitizing waved woodpecker

[*Celeus undatus* (Linnaeus, 1766)] (Fain and Aitken 1970). Therefore, our record of *T. strandtmanni* for South America, in brown-hooded gulls, is the first one for this host species, and the second one for Brazil.

In birds, nasal mites predominantly inhabit the upper respiratory tract, which can be considered the habitat for many of these parasitic species. Seabirds and shorebirds may provide different habitats to their nasal mites, as they may have slit-like nostrils (Charadriiformes, Gaviiformes, Pelecaniformes, Phaethontiformes, and Sphenisciformes), or tubular (Procellariiformes), nearly closed or vestigial (Pelecaniformes: Pelecanidae, and Suliformes: Fregatidae), or absent nostrils (Suliformes: Phalacrocoracidae and Sulidae) (Schreiber and Burger 2001, Zusi and Livezey 2006). Differences in the structure of the nasal passages in host bills may affect the ability of nasal mites to infect a host, based on differences between bird orders (Maa and Kuo 1965). Birds sampled in the current study had a wide variety of morphological characteristics in nostril openings and also in the structure of the nasal cavities, which influenced their parasitic indices. For example, 'Nostril height vs. Choana' width had a positive effect on the mean abundance of birds parasitized by nasal mites in the Bayesian models built. On the other hand, birds with vestigial or no nostrils were not parasitized by nasal mites. As the nostril serves as an entrance for the parasites, birds with a larger gateway (i.e. wider nostril) between and within species are more likely to be parasitized than birds with smaller nostrils.

We also found a weaker, but positive, effect of 'Culmen length vs. Choana length' on the abundance of mites. This reflects the habitat size provided by phylogenetically similar hosts to parasites, indicating that birds with larger nasal cavities are more heavily parasitized, consistent with expectations for species abundance and richness in ecosystems (MacArthur and Wilson 1967). Once parasitizing their hosts, nasal mites must survive and reproduce in their habitats (i.e. inside bird bills). In our study, we found a phylogenetic signal in bill morphology and a positive effect of 'Culmen length vs. Choana length' on the intensity of mites. If we trace an ecosystemic comparison and consider that larger habitats accommodate a higher number of individuals and species (MacArthur and Wilson 1967), then larger nasal cavities (i.e. more extensive habitats for mites) are expected to harbour a greater number of individuals within the host bill. Consequently, bill morphometry influences the mean intensity of nasal mites in bird hosts, and its dimensions are influenced by their phylogenetic relationship. We also found a weaker positive effect of 'Nostril height vs. Choana width' on the mean intensity of nasal mites, which reflects the relative size of the entry points of the parasites into their habitat. Therefore, birds with larger nasal openings are more likely to harbour higher parasite loads than those with narrower anatomical structures.

Host biology can also influence transmission and levels of parasitism. The time spent on colonies and in reproductive activities, including courtship, copulation, incubation, and chick rearing, varies among species. For Charadriiformes, kelp gull lays one to three eggs, incubated for ~27 days. Parental care continues until chicks reach ~14 weeks (Prellvitz *et al.* 2009). In terns, clutch size varies from one to three eggs, with incubation lasting about 23 days and fledging occurs after about 25 days. In the meantime, chicks still depend on parents for feeding, thermoregulation, and protection against predators (Savigny 2021). With a distinct biology, Magellanic penguins lay two eggs, incubate on the ground or in burrows for about 40 days, and raise their chicks for about 2 months (Borboroglu and Boersma 2015). In Procellariformes, the single egg is usually incubated longer than in other seabirds (i.e. *Thalassarche* 68–73 days and *Puffinus*, *Ardenna*, and *Calonectris* species 52–60 days of incubation). Fledging occurs at 72–167 days old (Savigny 2021). Due to the long periods spent at the colony (i.e. incubating and during parental care), seabirds may increase their chances of mite transmission, as there is longer close contact between individuals. Moreover, a bigger clutch size may increase the exposure and, consequently, the chances of parasitic transmission, as the frequency of provisioning increases in comparison to species with smaller clutch sizes. Finally, the mobility of the hosts (i.e. resident vs. migratory species or populations) may have a role in the frequency and patterns of exposure of hosts to mite infection (Hilario-Pérez and Dowling 2018). Therefore, the sampling site in the current study (tropical, subtropical, and temperate) may be an important factor in the infection and transmission of nasal mites. Studies with cosmopolitan species can be developed to control for morphological traits of hosts and account for the environmental and ecological differences of sampled individuals. Notwithstanding this, we cannot exclude the possibility of nasal mite infection occurring mainly or exclusively during the adult phase of hosts, which can be either through pair contact in courtship or through interspecific interactions in mixed flocks, at sea, in colonies, or on roosting sites.

Nasal mites on shorebirds and seabirds are poorly studied, which may be due to their wide distribution, difficulty in sampling, and host specificity. As a result, there is still considerable information about host–mite associations in shorebirds and seabirds that remains to be uncovered. In this study, novel host–mite records were reported, and several undescribed species were collected, some of which have already been described (Gastal *et al.* 2022, 2023), while others are awaiting formal descriptions. Certainly, more novel host association records and mite species will be uncovered as additional hosts are investigated. This study provides new insights into infection patterns and nasal mite diversity among shorebirds and seabirds, revealing potential anatomical influences on parasitism. Specifically, we found that bill-opening dimensions were positively associated with mean infection intensity and abundance, whereas overall bill morphology was not significantly related to prevalence. These results suggest that structural traits may influence parasite load, though they do not fully explain the observed host–parasite associations. A more comprehensive understanding of these interactions requires the analysis of additional factors, such as host reproductive biology, relationships among mites, and ecological variables like migratory behaviour and social organization.

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AUTHOR CONTRIBUTIONS

Silvia B. Gastal (study conception and design, sample and data collection, development of analysis protocol, preparation and identification of mites, original draft preparation, and manuscript review and editing), Cindy T. Barreto (statistical analysis, original draft preparation, and manuscript review and editing), Carolina S. Mascarenhas (preparation and identification of mites, manuscript review and editing, supervision), and Leandro Bugoni (study conception and design, manuscript review and editing, supervision).

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

S.B.G., C.T.B., C.S.M., and L.B. declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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DATA AVAILABILITY STATEMENT

Data will be made available on request to the corresponding author.

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