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The epidemiology of a novel *Leucocytozoon* parasite in an endangered population of marbled murrelets (*Brachyramphus marmoratus*) on the Oregon coast

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ABSTRACT

Parasitism is a known cause of morbidity and mortality in wildlife species and may exacerbate population declines in species threatened by changing landscapes. The marbled murrelet (*Brachyramphus marmoratus*) is an unusual seabird that forages in the ocean but uses trees in old growth and late successional forests for nesting. Populations have declined in some areas due to both changing ocean conditions and reduction in breeding habitat, making it important to consider the impacts of other factors, such as parasites and pathogens, on murrelet health and reproduction. In this study we describe a novel blood parasite (*Leucocytozoon marmoratus* sp. nov.*)* found in a murrelet population on the Oregon coast, USA and quantify its prevalence and burden in 374 individuals along the Oregon coast over a 6-year period. Genetic sequencing revealed that the species of *Leucocytozoon* we identified has a mitochondrial lineage most closely related to a *Leucocytozoon* found in yellow-eyed penguins (*Megadyptes antipodes*) of New Zealand. The prevalence of *Leucocytozoon* in murrelets was 62 % (233/374) and within an infected individual the mean burden of parasitism was 7.1 parasites/100 white blood cells, with substantial variation between individuals (from 1 to 113 parasites/100 white blood cells). Both parasite prevalence and burden varied across years and were higher in years of poorer ocean conditions suggesting that birds experiencing poor conditions may have had reduced ability to fight infection. Male murrelets had significantly lower parasite burdens than females, which may be due to energetic constraints of egg production in breeding females. Importantly, murrelets that did not attempt a nest were associated with higher parasite burdens at the time of capture, perhaps due to correlations between parasitism and systemic health.

1. Introduction

Leucocytozoon hemoparasites have been identified and described in numerous avian species, from raptors to songbirds to poultry (Morii, T., 1992; Marzal et al., 2005; Norte et al., 2009; Hanel et al., 2016; Granthon and Williams, 2017; Jiang et al., 2019). However, they have rarely been found in seabirds (Argilla et al., 2013; Parsons et al., 2017; Kleinschmidt et al., 2022). The clinical effects and implications for infected species have been shown to range greatly depending on the species infected, demonstrating the importance of investigating *Leucocytozoon* in all newly identified host species (Asghar et al., 2011).

Protozoans in the *Leucocytozoon* genus belong to the order Haemosporida which are part of the Apicomplexa phylum. *Leucocytozoon* shares the Haemosporida order with *Plasmodium*, the protozoan species that causes malaria in humans (Valkiūnas, 2004; Cepeda et al., 2021). Most *Leucocytozoon* are transmitted by a black fly (family: Simuliidae) with only one species having *Culicoides* midges as vectors (family: Ceratopogonidae) as its vector (Wernery, 2016). Black fly development involves four life stages, three of which are dependent on fresh running water sources from small creeks to rivers (Currie and Adler, 2008; Cunze

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et al., 2024). Factors such as water temperature, current rate, vegetation, food material, and oxygen content of the water sources determine where eggs are deposited, and thus determine the distribution of terrestrial adult flies (Zahar, 1951).

Leucocytozoon are obligate heteroxenous parasites, meaning their life cycle requires two distinct host species to be completed. The parasite undergoes part of its development in the definitive host, a blood-sucking vector, before continuing its life cycle in the intermediate host, a bird (Valkiūnas, 2004). Within the fly host, both the sexual processes of gametogenesis and fertilization occur as well as the asexual multiplication of sporogony (Valkiūnas, 2004); these developmental stages take no longer than 3–4 days. Once the *Leucocytozoon* develops into the infective stage of a sporozoite, they move into the salivary glands of the fly to be transmitted to the host species during the next blood meal (Valkiūnas, 2004). After being transferred to the bird host they enter the liver parenchymal cells and undergo further asexual development, dividing to form merozoites (Valkiūnas, 2004). These merozoites are subsequently released into the bloodstream and can infect red blood cells, white blood cells, and/or thrombocytes. Some of these merozoites develop into gametocytes and are ingested by the next feeding fly to continue the life cycle (Valkiūnas, 2004). *Leucocytozoon* parasites can persist within their avian host in an exo-erythrocytic tissue stage for the entirety of the bird's lifespan, though the mechanism underlying this persistence is not understood (Valkiūnas, 2004). The persistent exo-erythrocytic tissue stage results in relapse of parasitemia in a bird due to stimulation of merozoite production. This stimulation is thought to be seasonal, with fluctuations in parasitemia associated with warmer seasons that favor the vector species (Valkiūnas, 2004; Valkiūnas and Iezhova, 2023). Over 80 species of *Leucocytozoon* have been identified, but it is suggested this is a small proportion of the actual number based on ongoing taxonomical work (Peirce, 2005; Harl et al., 2020).

Leucocytozoonosis has been known to cause high levels of mortality in domestic turkey, waterfowl, and chicken populations. In two isolated incidents, one in the 1950s and one in the early 1970s, *Leucocytozoon* infections had widespread negative impacts on the turkey industry. This degree of mortality from leucocytozoonosis has only been documented in commercial flocks and never in wild bird populations. It is postulated that leucocytozoonosis only has the catastrophic effects and mortality rates seen with poultry under high-density conditions when individuals are housed together in environments favorable for the vector species (Barnett, 1977; Adler and McCreadie, 2019). Thus, previous studies investigating *Leucocytozoon* infections in wild bird populations have focused primarily on characterizing each new species of parasite and quantifying their presence in a population (Argilla et al., 2013; Dezfoulian et al., 2013; Jiang et al., 2019). Several studies have emphasized impacts of parasitism on body condition score, reproductive success, and various blood parameters in species such as the American redstart (*Setophaga ruticilla*), gray catbird (*Dumetella carolinensis*), cedar waxwing (*Bombycilla cedrorum*), red-eyed vireo (*Vireo olivaceus*) (Granthon and Williams, 2017), house martin (*Delichon urbica)* (Marzal et al., 2005), and great tit (*Parus major)* (Norte et al., 2009).

This is the first study evaluating leucocytozoonosis in the marbled murrelet (*Brachyramphus marmoratus*, hereafter murrelet) a seabird in the auk family (Alcidae) that is found along the Pacific coast from Alaska to Northern California. Murrelets spend most of their lives on the ocean, but during their breeding season they can travel more than 85 km inland to nest (Nelson and Hamer, 1995; Lorenz et al., 2017; Nelson, 2020). In the northern part of their range in Alaska they can nest on the ground; however, in the southern part of their range they nest solely in trees within late-successional and old growth forests. Specifically, each female lays her single egg on a large diameter, horizontal, moss-covered limbs of older trees (DeSanto and Nelson, 1995; Ralph et al., 1995). Murrelets are often observed in pairs at-sea, and Sealy (1975) found that birds in pairs were often male and female and thought to be mated pairs. There is evidence of murrelets occupying the same forest stands for at least 40 years (Divoky and Horton, 1995; SKN, unpubl. data). Their distinctive lifestyle means they contend with both changing ocean conditions (Becker and Beissinger, 2006; Betts et al., 2020) as well as factors that reduce their nesting habitat quality (Raphael et al., 2016; Valente et al., 2023). Murrelets are listed as threatened under the Federal Endangered Species Act (United States Fish and Wildlife Service, 1997). They were listed in the state of Oregon as threatened starting in 1992 but were reclassified as endangered in 2021. Although Oregon and California populations are thought to be stable (McIver et al., 2025), Washington state populations are experiencing a concerning decline (Miller et al., 2012; McIver et al., 2025). This is attributed to negative effects of ocean conditions on prey availability, fragmentation and loss of nesting habitat, and high rates of nest predation (Becker and Beissinger, 2006; Raphael et al., 2016; Betts et al., 2020; Valente et al., 2023).

As part of an extensive, long-term study on marbled murrelets in Oregon (Garcia-Heras et al., 2024), blood smear analyses were conducted to assess overall health and physiological condition. Preliminary blood smear analysis identified a *Leucocytozoon* hemoparasite in a population of murrelets on the Oregon Coast (Ryan, 2024). No prior studies have described *Leucocytozoon* in murrelets, and these hemoparasites are rarely reported in other seabird species (Parsons et al., 2017; Kleinschmidt et al., 2022). Here, we: (1) describe the *Leucocytozoon* found in individuals in the population along the central Oregon coast, (2) determine *Leucocytozoon* prevalence and burden, and (3) quantify how *Leucocytozoon* infection is correlated with body condition or breeding propensity. We predict that higher rates of infection will be observed in murrelets with poor body condition and in years of poor ocean conditions, as reduced energy reserves may weaken immune function, making individuals more susceptible to parasitic infections (Demas, 2004). Additionally, we predict that infected individuals will attempt fewer nests, as the physiological burden of parasitism may reduce their ability to invest in reproduction.

2. Materials and methods

2.1. Murrelet capture, measurements, and sample collection

We undertook field data collection from late April to early June during 2017–2019 and 2021–2022. We examined 374 live marbled murrelets over the course of five years of captures. To do this we captured birds at-sea during the night in nearshore areas within 35 km north or south of the coastal city of Newport, Oregon. Working from a large vessel, we offloaded a small inflatable boat that searched for birds with a high-powered spotlight and used a large dip net to capture birds (Whitworth et al., 1997). Immediately after capture, each bird was placed in a plastic transport container and then transported to the research vessel for processing. Once on the research vessel, we placed a uniquely numbered U.S. Geological Survey metal band on one of the bird's legs and then measured body mass (±1 g) and culmen length (±0.1 mm). Each bird's tarsus was measured with calipers from the intertarsal joint anteriorly to the distal end of the last leg scale to the nearest 0.1 mm. We then took a small sample of blood from the medial metatarsal vein for parasite assessment and for DNA sexing, as murrelets are not sexually dimorphic in size or plumage so sex cannot be determined in the hand. For individuals that weighed ≥200 g, we also attached a small VHF telemetry tag (model A4330, 2.5 g, Advanced Telemetry Systems, Isanti, MN, US) to the upper back using a subcutaneous anchor (Newman et al., 1999). We released all birds within 1 h of capture and within 1 km of their original capture location.

After release, we tracked radio-tagged birds by fixed wing aircraft and via 72 ground-based, fixed telemetry stations that were located every 2–3 km across our 135 km study area, stretching from Pacific City, Oregon southward to Florence, Oregon (Garcia-Heras et al., 2024). Using both methods, we tracked birds on a near-daily basis and thus were able to detect the distinct movement patterns murrelets exhibit when incubating eggs, switching between the marine environment for

foraging and the terrestrial environment for incubation every other day (Bradley et al., 2004), which we deem nesting propensity in our analyses. Birds that were showing the distinctive movement patterns any time during the subsequent 8 weeks after sampling were encoded as "attempted to nest", whereas birds that never show these distinctive movement patterns were encoded as "no attempts to nest". Nesting success was not used as a variable due to low sample size, only nesting attempts were included.

2.2. Body condition index

To adjust for overall body mass, we calculated a body condition index (BCI) based on mass-length residuals. These residuals were calculated from a linear regression between body mass and tarsus length. A negative residual indicates a bird whose body mass is lower than expected for its size, whereas a positive residual indicates a bird whose body mass is larger than expected based on its size. Residuals can be confounded by sex due to variation in BCI between males and females (Green, 2001; Labocha and Hayes, 2012), so we calculated residuals separately for males and females.

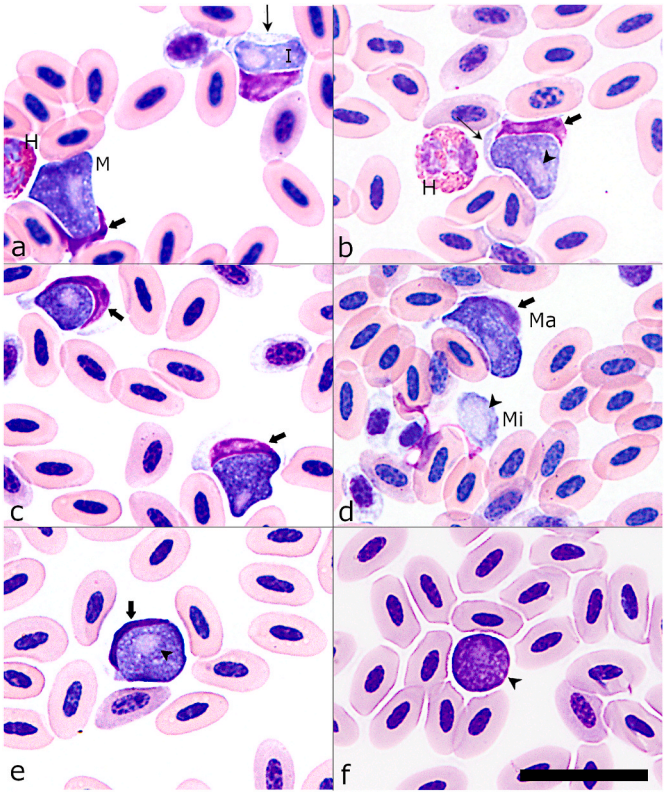

Fig. 1. *Leucocytozoon marmoratus* sp. nov. from the blood of a marbled murrelet (*Brachyramphus marmoratus*). **a.** Developing macrogametocyte (M) with densely stained, granular cytoplasm within host cell with flattened nucleus and no visible cytoplasm next to a host heterophil (H). Immature (I) macrogametocyte with visible remnant host cell cytoplasm and deformed host cell nucleus (HCN). **b.** Macrogametocyte with ovate nucleus (arrow head). Host cell cytoplasm is observed surrounding the parasite (long, thin arrow) and HCN elongated around the periphery (short arrow). Host heterophil (H) is visible. **c.** Immature macrogametocytes developing within host cell cytoplasm. Remnants of host cytoplasm are visible surrounding crescent-shaped HCN. **d.** Microgametocyte (Mi) with lightly stained cytoplasm and nucleus with poorly defined boundary (arrow head). Mature macrogametocyte (Ma) with densely stained cytoplasm. Host cell cytoplasm is scant and HCN can be seen protruding from periphery of cell (short arrow). **e.** Thin HCN (short arrow) pushed to the periphery of the rounded cell by appressed mature macrogametocyte (arrow head). **f.** Rounded, fully-developed gametocyte in enucleated host cell (arrow head). Modified Wright stained thin-blood films. Scale bar = 20 μm.

2.3. Blood smear preparation and evaluation

At the time of capture, one drop of collected whole blood was used to make a blood smear for each bird. Blood smears were air dried and stored up to one week before being transferred to the Oregon Veterinary Diagnostic Laboratory at Oregon State University for analysis. Slides were fixed with methanol and stained using a modified Wright stain (Hematek stain pack, Siemens Healthineers, Erlangen, Germany). The stained slides were examined using an Olympus BX43 microscope. Preliminary blood smear analysis of these birds revealed a parasite, which was identified as a member of the *Leucocytozoon* genus.

Evaluation of each slide included both presence and burden. Presence of parasites was recorded if at least one parasite was seen in the monolayer of the smear. To quantify the burden of parasites we counted the number of parasites seen while counting 100 white blood cells (WBCs). For birds in which 100 WBCs could not be found, we used the number found in the counted number of WBCs and extrapolated to 100 WBCs. When evaluating for parasite presence and burden, all blood smears were analyzed blind with respect to the main factors analyzed in our study, including year, birds that were male vs. female, or breeders vs. non-breeders.

The sample sizes used to quantify *Leucocytozoon* prevalence (n = 374) and *Leucocytozoon* burden (n = 196) differed for several reasons. Slides were not included in the burden study if they were uninfected (n = 141), if slide quality was too poor to perform accurate counts (n = 30), or if the slide was misplaced between prevalence and burden counting (n = 7). In summary we included 374 birds in prevalence analyses, and 196 birds in burden analyses. Digital images of parasites were taken using an oil immersion lens at 100X power field.

2.4. Molecular sexing methods

Genetic sex determination was conducted at Oregon State University in the Epps lab. DNA extraction was performed using the Qiagen (Valencia, CA, USA) QIAamp protocol, and sexing was performed according to methods described by Fridolfsson and Ellegren (1999).

2.5. Amplification and sequencing of parasite mitochondrial DNA (mtDNA)

Extracted DNA from three individuals with high parasite burdens as determined by blood smears was used for amplification and sequencing. A nested PCR was performed using primers specific to the cytochrome *b* gene of the mitochondrial genomes of apicomplexan genera *Plasmodium, Haemoproteus*, and *Leucocytozoon* according to the methods of Hellgren et al. (2004). Briefly, an initial PCR was performed using the primers HaemNF1 (5′-CATATATTAAGAGAAITATGGAG-3′) and HaemNR3 (5′-ATAGAAAGATAAGAAATACCATTC -3′), using the following reaction conditions: An initial denaturation step of 94° C for 2 min followed by 30 s at 94° C, 30 s at 50° C, and 45 s at 72° C for 20 cycles, and a single step of 72° C for 10 min. We used 2 μl of this reaction to perform a second PCR using primers specific to *Leucocytozoon*, HaemFL (5' -ATGGTGTTTTAGATACTTACATT -3′) and HaemR2L (5′- CATTATCTG-GATGAGATAATGGIGC -3′) with the same thermocycling protocol. The resulting PCR products were visualized using a 0.8 % agarose E-gel Clonewell II (Life Technologies, Carlsbad, CA, USA) and single bands of ~500 bp were retrieved from the recovery well. Products from three samples were sequenced in both directions using the primers HaemFL and HaemR2L on an ABI Prism 3730 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) at the Center for Quantitative Life Sciences at Oregon State University.

2.6. Phylogenetic analysis

The resulting sequences from murrelet samples were assembled and aligned with similar partial cytochrome *b* gene sequences obtained from

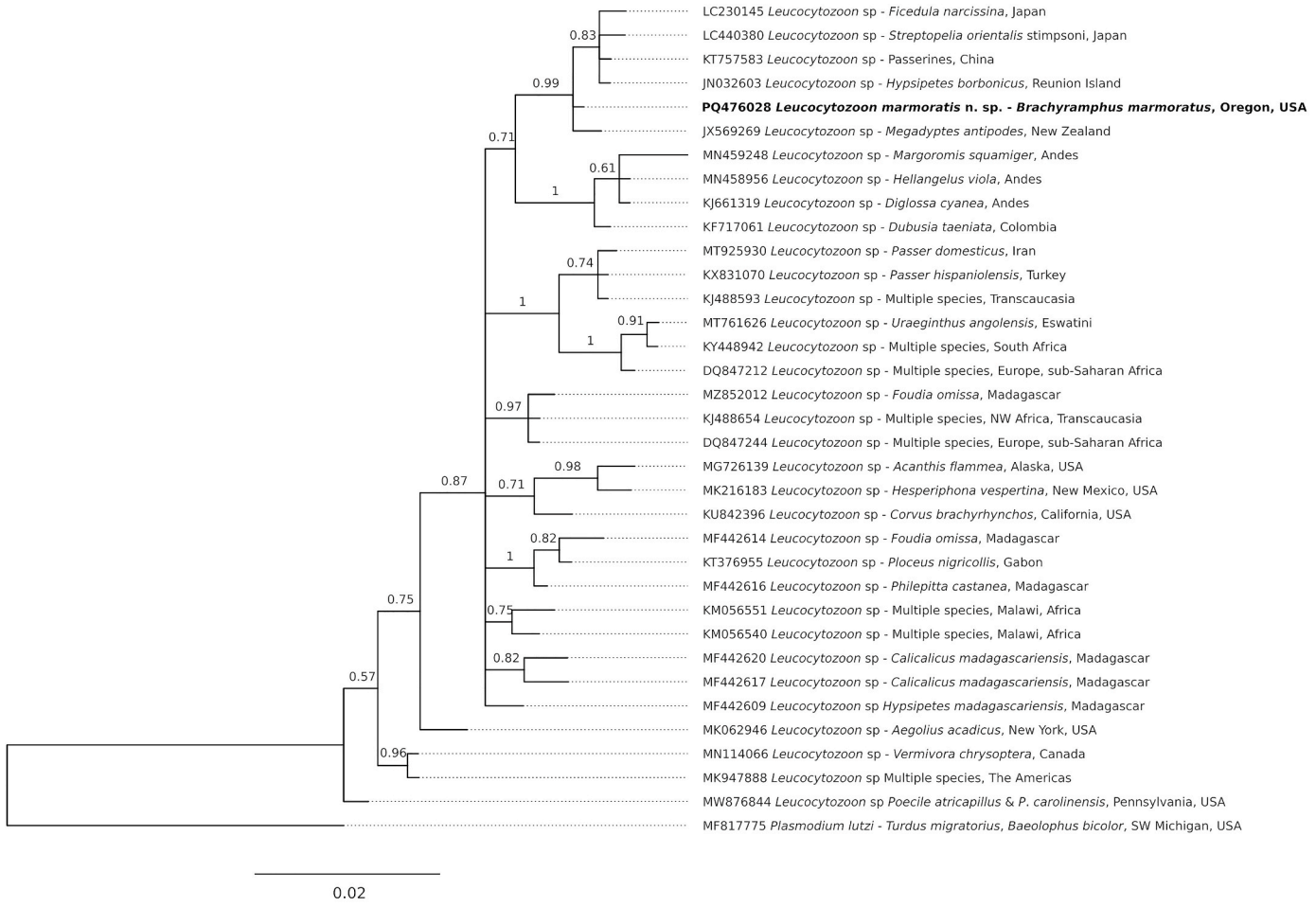

Fig. 2. Bayesian phylogenetic reconstruction based on partial mitochondrial cytochrome *b* sequences (478bp) from *Leucocytozoon* spp. obtained from GenBank. *Leucocytozoon marmoratus* n. sp. is indicated in bold. *Plasmodium lutzi* was used as an outgroup taxon. GenBank accession numbers, documented host species, and geographic location for each are shown. Branch values are posterior probabilities, scale bar show substitutions per site.

the NCBI GenBank database using the BLASTN search tool: https://blast.ncbi.nlm.nih.gov/. A total of 33 closely related *Leucocytozoon* spp. sequences were selected and aligned with the sequence obtained from murrelets using MUSCLE v5.1 (Edgar, 2004). The resulting 478 bp alignment was analyzed using ModelTest v.2.1.4 (Darriba et al., 2012) to determine the best-fit nucleotide substitution model. A phylogenetic reconstruction was made using MrBayes v3.2.6 (Hueselbeck et al., 2001)) using a general time-reversible model with gamma-distributed rate variation across sites (GTR + G) and *Plasmodium lutzi* as an outgroup. MrBayes was run for 2,000,000 generations and sampled every 1000 generations, with 500,000 generations discarded as burn-in.

2.7. Statistical analyses

Samples were collected over a 6-year period, so we first evaluated whether there was annual variation in parasite prevalence or burden using a non-parametric ANOVA and Dunnetts multiple comparisons in GraphPad Prism. Parasite prevalence and burden varied across years so year was included in all subsequent analyses. To assess whether sex, body condition index, or nesting propensity related to the likelihood a murrelet was infected with parasites, we performed a multiple logistic regression in R using the glmer function with parasite presence as the dependent variable. All numeric variables were rescaled using the scale function in the MASS package, whereas year was included in the model as a random effect. The formula appears as: glmer(Prevalence ~ Intercept + (1|Year) + Sex + scale(Body Condition Index) + Nesting, family = binomial(link = "logit)). To evaluate whether burden related to any of those same parameters we used a negative binomial regression in R using the glmer.nb function with burden as the dependent variable. Again, all numeric variables were rescaled using the scale function and year was included as a random effect. The formula appears as: glmer.nb (Burden ~ Intercept + (1|Year) + Sex + Body Condition Index + Nesting).

3. Results

3.1. Parasite description

Leucocytozoon macrogametocytes and microgametocytes were visually identified in stained peripheral blood smears. Immature microgametocytes were observed in amorphous to rounded host cells (Fig. 1a–d) with densely staining, vacuolated cytoplasm. In infected cells, the host cell nucleus was arranged around the periphery of the cell and cap-like, or thickened in the center. Microgametocytes (Fig. 1d) were rarely observed and had lightly stained cytoplasm and a large, diffuse nucleus. Mature gametocytes (Fig. 1e) were rounded in apparently enucleated host cells.

Phylogenetic reconstruction of partial cytochrome *b* gene sequences from closely related *Leucocytozoon* spp. (98.3 % average identity) placed *L. marmoratus* n. sp. in a clade with 5 *Leucocytozoon* spp. (Genbank numbers: JX569269-New Zealand (99.8 % identity), JN032603-Reunion Island (99.8 % identity), KT75783-North China (99.8 % identity), LC230145-Japan (99.5 % identity), and LC4400380-Japan (99.5 % identity), obtained from *Megadyptes antipodes* (Sphenisciformes),

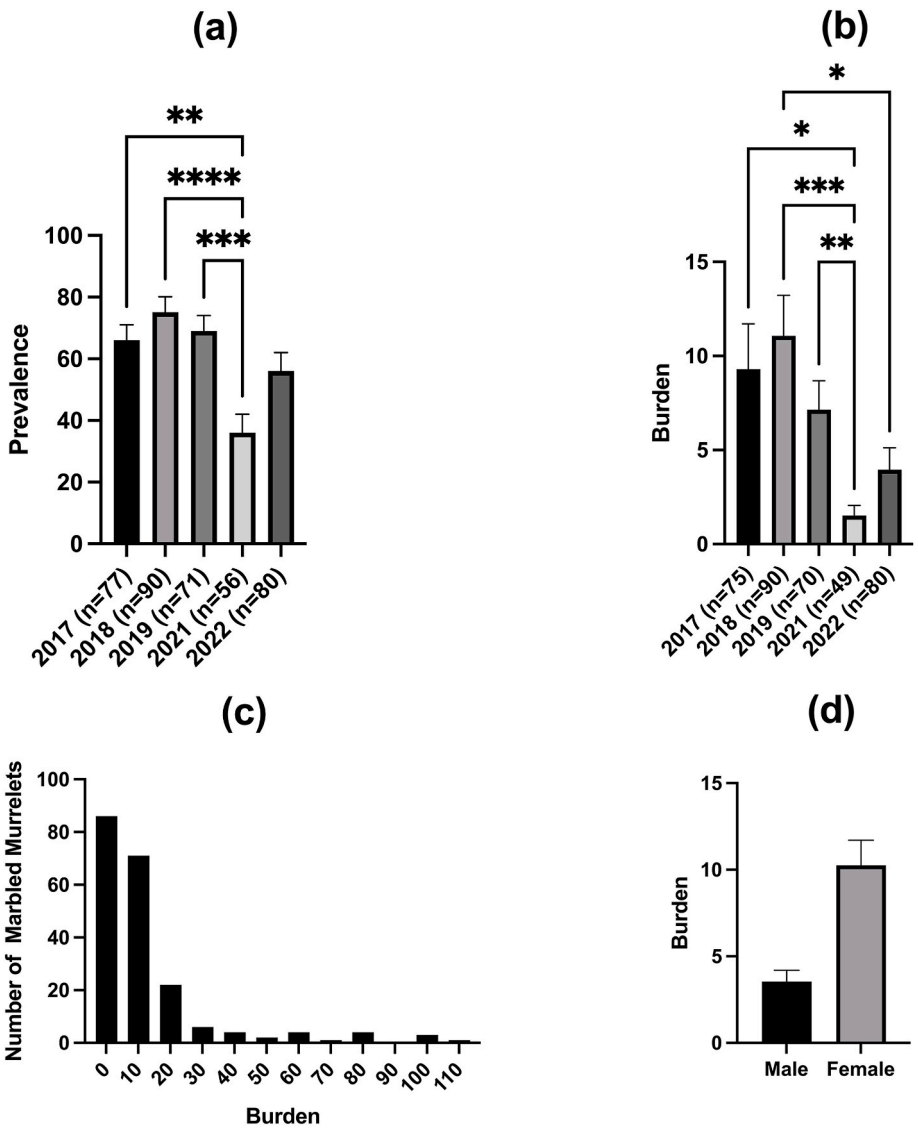

Fig. 3. Epidemiology. (a) Prevalence of parasitism of birds captured varied by year. (b) Average parasite burden varied by year (c) A frequency distribution showing the degree of parasitism in the murrelet population. (d) Females had greater *Leucocytozoon* burdens than males. See Table 1 for full statistics. Stars represent $p < 0.05$.

Hypsipetes borbonicus (Passeriformes), passerine but species not specified (Passeriformes), *Streptopella orientalis stimpsoni* (Columbiformes), and *Ficedula narcissina* (Passeriformes), respectively.

3.1.1. Taxonomic summary (Fig. 2)

Leucocytozoon marmoratus n. sp. (Alveolata: Apicomplexa: Aconoidasida: Haemosporida: Leucocytozoidae).

Type host: Marbled murrelet (Brachyramphus marmoratus).

Vectors: Currently unknown.

Representative sequences: Partial mitochondrial cytochrome *b* gene sequence was submitted to Genbank, accession number PQ476028.

Type locality: Nearshore area 35 km north and south of Newport, Oregon, USA.

Site of infection: Blood cells; Origin is unclear.

Prevalence of infection: In type locality, 233 of 374 (62 %) were infected as determined by microscopic examination.

Etymology: Species epithet refers to host from which type specimen was obtained, *B. marmoratus*.

3.2. Epidemiology

Of the 374 murrelet blood smears evaluated for prevalence, 233 birds were detected having parasites (62 % prevalence). *Leucocytozoon* prevalence ranged from 36 % to 76 % of the individual captured per year, with the years of 2017-19 having the highest prevalence values. (Fig. 3a, Table 3, $p < 0.001$, $F = 7.009$, $n = 374$). Blood smears that were positive for *Leucocytozoon* had an average burden of 7.1 parasites/100 WBCs (range 1–113, CI 95 %, n = 203). Average parasite burden per year ranged from 1.52 to 11.07 parasites/100 WBC and the annual variation showed the same pattern as prevalence, with higher burdens in 2017–19. (Fig. 3b–Table 4, $p = 0.001$, $F = 4.587$, $n = 364$). We detected

Table 1
Negative binomial regression for parasite burden in marbled murrelets sampled along the central Oregon coast. Table shows the estimate from the negative binomial regression with the corresponding standard error and p-value. Regression formula is shown on the first row of the chart. If the variable is categorical the reference variable is shown in brackets.

Variable	Estimate	Standard Error	p value
Intercept	2.164	0.297	<0.001
Sex [M]	−0.872	0.255	0.006
Body Condition	0.236	0.124	0.057
Nesting Y/N [Y]	−0.910	0.124	0.028

Table 2
Multiple logistic regression for parasite prevalence. Table shows the parameter estimates from a multiple logistic regression with the corresponding standard errors and p-values. The regression formula is shown on the first row of the chart. If the variable is categorical the reference variable is shown in brackets.

Variable	Estimate	Standard Error	p value
Intercept	0.365	0.327	0.264
Sex [M]	−0.124	0.274	0.651
Body Condition Index	0.485	0.150	0.001
Nesting Y/N [Y]	−0.478	0.442	0.279

Table 3
Parasite prevalence varied by year based on an ANOVA ($p < 0.001$, $F = 7.009$, $n = 374$). A Dunnett's T3 Multiple Comparisons test shows which years were different from each other, with bolded comparisons having a $p < 0.05$. Sample sizes are listed in parentheses.

Years Compared	Mean Difference	Adjusted p value
2017 (n = 77) vs. 2018 (n = 90)	−9.0	0.895
2017 (n = 77) vs. 2019 (n = 71)	−3.0	0.999
2017 (n = 77) vs. 2021 (n = 56)	**30.0**	**0.002**
2017 (n = 77) vs. 2022 (n = 80)	10	0.891
2018 (n = 90) vs. 2019 (n = 71)	6	0.993
2018 (n = 90) vs. 2021 (n = 56)	**39**	**<0.001**
2018 (n = 90) vs. 2022 (n = 80)	19	0.148
2019 (n = 71) vs. 2021 (n = 56)	**33**	**<0.001**
2019 (n = 71) vs. 2022 (n = 80)	13	0.637
2021 (n = 56) vs. 2022 (n = 80)	−20	0.180

Table 4
Parasite burden varied by year based on an ANOVA ($p = 0.0014$, $F = 4.587$, $n = 364$). A Dunnett's T3 Multiple Comparisons test shows which years were different from each other, with bolded comparisons having a $p < 0.05$.

Years Compared	Mean Difference	Adjusted p-value
2017 (n = 75) vs 2018 (n = 90)	−1.780	0.999
2017 (n = 75) vs 2019 (n = 70)	2.150	0.997
2017 (n = 75) vs 2021 (n = 49)	**7.770**	**0.024**
2017 (n = 75) vs 2022 (n = 80)	5.330	0.391
2018 (n = 90) vs 2019 (n = 70)	3.930	0.770
2018 (n = 90) vs 2021 (n = 49)	**9.550**	**0.0004**
2018 (n = 90) vs 2022 (n = 80)	**7.110**	**0.041**
2019 (n = 70) vs 2021 (n = 49)	**5.620**	**0.009**
2019 (n = 70) vs 2022 (n = 80)	3.180	0.649
2021 (n = 49) vs 2022 (n = 80)	−2.440	0.449

a negative binomial distribution for parasite burden in our population, with more birds having light parasite burdens and fewer being heavily parasitized (Fig. 3c). Males had significantly lower *Leucocytozoon* burdens compared to females (Fig. 3d–Table 1, $p < 0.001$).

3.3. Correlations between parasitism and measures of BCI and breeding propensity

Individuals in better condition as measured by BCI did not have altered parasite burdens (Table 1), but they were more likely to have parasites present (Fig. 4a, Table 2). *Murrelets that were less likely to attempt a nest were associated with higher parasite burdens at the time of capture, whereas murrelets that were more likely to attempt a nest were associated with lower parasite burdens at the time of capture.* (Fig. 4b–Table 1).

4. Discussion

4.1. Parasite description

Comparison of the partial cytochrome *b* gene sequence from the *Leucocytozoon* isolated from sampled murrelets to those in existing sequence databases confirmed that the *Leucocytozoon* species present in the sampled birds is a novel parasite. Our phylogenetic tree shows that the *Leucocytozoon* species found in this murrelet population is most closely related to a *Leucocytozoon* species in the yellow-eyed penguin (*Megadyptes antipodes*) of New Zealand. Other closely related species are primarily forest birds that inhabit moist forests. To our knowledge, this is the first description of a *Leucocytozoon* species in a member of the seabird family Alcidae.

4.2. Epidemiology

As expected *Leucocytozoon* burden and prevalence was higher in years of poor ocean conditions (2017-19) and lower in years of better ocean conditions (2021-22). A marine heatwave event between 2014 and 16 (Bond et al., 2015) altered prey communities including murrelet prey items (Gomes et al., 2024) that had lasting effects through 2019 and caused multiple seabird mortality events (Jones et al., 2023). In 2020, ocean conditions began to improve (Thompson et al., 2024), and 2021 included some of the best ocean conditions in nearly a decade for upper trophic level predators like murrelets (Thompson et al., 2022). Importantly, *Leucocytozoon* cause a persistent infection, so once infected the animal does not clear infection but instead infection persists in tissues of the bird which can then result in a relapse of parasitemia when conditions for the parasite are good or when the bird does not have the energy to invest in immune responses to control the infection. Taken together, this suggests that in times of poor forage availability they may be unable to limit their *Leucocytozoon* infection burden due to energetic constraints resulting in increased parasitemia. However, future research should investigate how variation in ocean conditions and forage availability directly impact parasite burdens in murrelets to better understand this pattern.

Leucocytozoon burdens were on average higher in female murrelets than male murrelets, which may be due to energetic constraints that limited the ability of females to limit *Leucocytozoon* infection burden. Captures and data collection took place at the beginning of the murrelet breeding season, so it is possible that during this time female birds have altered physiology with much of their energy reserves going toward reproductive effort. Because egg formation in murrelets is such an energy-costly process, replication of the *Leucocytozoon* parasite could be more rapid if energy is diverted away from the body's immune responses. Adequate energy storage and metabolism capabilities are necessary to mount an immune response (Demas, 2004), and murrelets with higher burdens had altered immune function compared to those with lower burdens (Ryan, 2024). Males do not require energy allocation to egg formation and this might explain why males had lower parasite burdens during this part of the breeding season (Ilmonen et al., 2002; Williams, 2005).

4.3. Correlations between parasitism and measures of BCI and breeding propensity

Unexpectedly, we found there was an association between having a parasite infection and having a higher body condition but there was no relationship between parasite burden and body condition. It is possible that birds with low body condition and high burdens were more likely to undergo mortality, reducing the number of animals with low body condition and high burdens. Thus, one fruitful avenue for future investigation is to focus on assessing whether this *Leucocytozoon* influences survival rates of infected murrelets. However, an alternative explanation could be that only older sexually mature birds are infected and older birds may have higher body condition. This hypothesis is based on the notion that murrelets have delayed sexual maturity and begin nesting ≥3 years post-hatching, similar to other auks (DeSanto and Nelson, 1995; Hébert et al., 2006). Thus, once murrelets reach sexual maturity and begin nesting inland, they then may be exposed to presumed fly

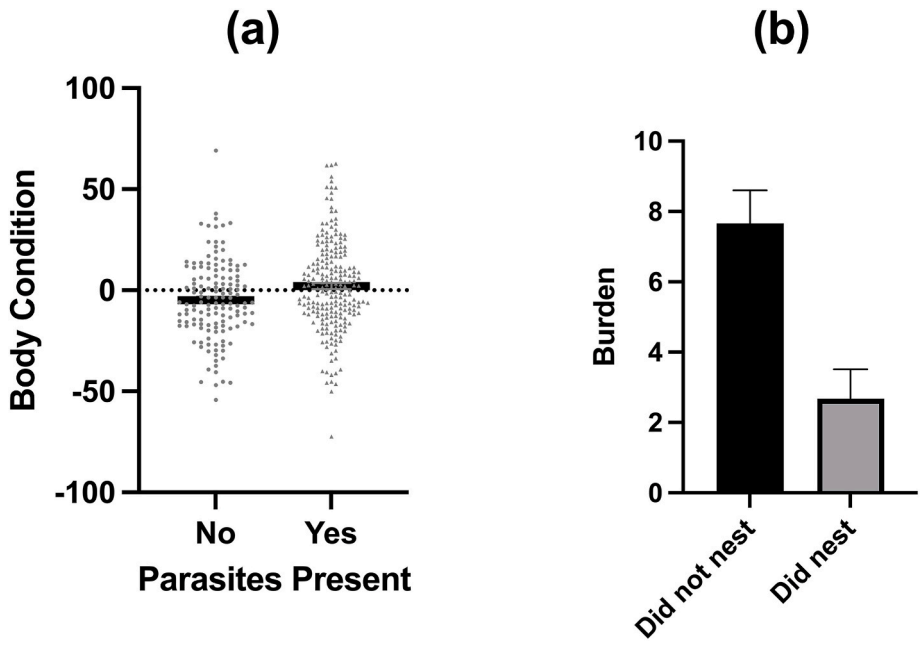

Fig. 4. Correlates of parasitism. (a) Individuals with a greater body condition were more likely to have *Leucocytozoon* parasites present ($p = 0.004$). See Table 2 for details of statistical analysis. (b) Marbled murrelets that subsequently nested that year had lower parasite burdens than murrelets that did not subsequently nest that year ($p < 0.001$). See Table 1 details of statistical analysis.

vector and become infected with *Leucocytozoon*. This idea merits further study to determine the route(s) of infection that occur.

As predicted, *murrelets that were less likely to attempt a nest were associated with higher parasite burdens at the time of capture*. On average, murrelets captured during years of poor ocean conditions had greater parasite burdens and were less likely to nest. One explanation for this finding is that food availability for pre-nesting murrelets affected both parasite burdens and the propensity for nesting. Parasite burden itself could have also affected nesting propensity because individuals with leucocytozoonosis were not healthy enough to either make an egg or attempt to nest. Parasites can weaken the avian host, reducing the ability of the bird to forage for food which would directly impact the production of an egg (Asghar et al., 2011). Mounting an immune response can involve secondary damage due to a non-specific inflammatory response, oxidative stress, and auto-immunity, all of which can damage host cells (Sorci and Faivre, 2009). Depression of immune responses has been demonstrated in human malarial infections, with research showing impairment of multiple components of both the innate and adaptive immune systems, and in chickens with leucocytozoonosis (Valkiunas & A lezhova 2023). Not only does this hinder the host's response to the malarial infection, but it can also predispose them to secondary infections that further weaken the host (Bonagura and Rosenthal, 2020). Birds with more severe parasitemia may choose to conserve resources and not attempt to make a nest so that resources can be partitioned to immune responses. It is important to note that birds with higher parasite counts are unlikely to merely be subadults that have not nested yet, as murrelets do not begin to spend significant time inland, in the environment of the presumed vector, until they are sexually mature. Overall, individuals that were less likely to attempt a nest were associated with higher parasite burdens at capture, and the prevalence of severe parasitemia is greater during years when ocean conditions are poor and murrelet food is relatively scarce. Future research should evaluate the extent to which parasitism influences the reproductive success and overall fitness of marbled murrelets.

4.4. Conclusion

We demonstrated that murrelets are commonly infected by a newly described blood parasite, that higher levels of parasitemia are more likely to occur when birds are energy restricted during poor environmental conditions, and that parasite infection may correlate with the likelihood of nesting. Continued research is integral to identify how changing ocean conditions, deforestation, and infectious diseases interact to affect this endangered species.

CRediT authorship contribution statement

Miranda Michlanski: Writing – original draft, Investigation, Formal analysis, Data curation. **Jonathan Dachenhaus:** Writing – review & editing, Investigation, Data curation. **Jennifer Johns:** Writing – review & editing, Methodology, Investigation. **S. Kim Nelson:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization. **Shannon Phelps:** Writing – review & editing, Methodology, Investigation. **James W. Rivers:** Writing – review & editing, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Daniel D. Roby:** Writing – review & editing, Funding acquisition, Conceptualization. **Ethan Woodis:** Writing – review & editing, Investigation, Data curation. **Kelsey Ryan:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Lindsay J. Adrean:** Writing – review & editing, Investigation. **Justin L. Sanders:** Writing – review & editing, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis. **Brianna R. Beechler:** Writing – review & editing, Visualization, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Conflict of interest

There are none to declare.

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