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A SURVEY OF ENDOHELMINTH DIVERSITY OF BIRDS COLLECTED IN THE SAN FRANCISCO BAY AREA

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Wildlife rehabilitation

ABSTRACT

The helminth fauna of birds has been the focus of many parasitological studies, which illustrate the especially diverse nature of avian helminth communities. In this study, we investigated the species richness, identity, and abundance of helminth infections in 17 species of birds representing 6 orders from the San Francisco Bay Area of California. A total of 70 birds were provided by wildlife rehabilitation centers and hunting groups from 13 California counties. Helminths were identified morphologically to the lowest taxonomic level, and, whenever possible, trematode identifications were confirmed using large ribosomal subunit (*28S*) rDNA sequences. Eighty-seven percent of birds were infected with helminths, including 86% infected with nematodes, 36% with trematodes, and 16% with either cestodes or acanthocephalans. We identified 39 helminth taxa, including 15 nematodes, 15 trematodes, 5 cestodes, and 4 acanthocephalans, which resulted in 33 new geographic records and 22 new host records. Among the orders of birds dissected, the Anseriformes Wagler, 1831, supported the highest total richness of helminths (18 taxa), although the highest helminth richness values in individual host species were observed in *Nycticorax nycticorax* (black-crowned night heron) L., 1758, and *Ardea herodias* (great blue heron) L., 1758, both with 7 taxa. *Nycticorax nycticorax* was also infected with *Ribeiroia ondatrae* (Price, 1931), which represents a new definitive host record in the United States. Our results demonstrate the need to generate baseline helminth survey data, which can be used to help understand the knowledge gaps for parasite life cycles, as well as patterns of parasite distribution.

With more than 10,000 species worldwide, birds represent a widespread group of hosts for many helminth parasites and can act as an important helminth dispersal mechanism (Rausch, 1983; Crompton, 1997; Leung and Koprivnikar, 2016). Among vertebrates, birds are of particular interest in parasitology due to the many factors that influence the prevalence of infection (Rausch, 1983; Crompton, 1997; Poulin and Mouillot, 2004; Atkinson et al., 2009; Gutiérrez et al., 2017). First, many avian hosts have a diverse diet that exposes them to numerous trophically transmitted parasites (Leung and Koprivnikar, 2016; Skirnisson, 2016). Thieltges and Poulin (2016) determined that a bird's prey range had a positive effect on parasite species richness. Second, avian hosts that forage in multiple habitats, such as freshwater and marine environments, also tend to have higher parasite richness (Leung and Koprivnikar, 2016; Gutiérrez et al., 2017). For example, Gutiérrez et al. (2017) found that charadriiform hosts that used both freshwater and saltwater habitats supported 68% higher helminth richness than those species found in only a single habitat. Finally, the migratory behaviors of many birds often expose them to, and result in the acquisition of different parasite communities during travel (Koprivnikar and Leung, 2015; Barton and Sandercock, 2018; Gutiérrez et al., 2019; Vestbo et al., 2019). In an analysis of the nematode diversity in birds, Leung and Koprivnikar (2016) reported that migratory birds hosted a nearly 3-fold more speciose nematode community than those from nonmigratory bird species. These observations underscore the importance of parasitological surveys that encompass bird host species with variable diets, habitat usage, and migratory behaviors.

Relatively few studies have surveyed the helminth communities from birds found in California. Despite the wide variety of

habitats (marine, freshwater, urban, desert, mountain, and others) found in the state and its position along the Pacific Flyway migratory route, only 4 studies have used hunting or opportunistic collections of avian hosts to study helminth communities over the past 60 yr (Matthias, 1963; Ching, 1990; Baker et al., 1996; Hannon et al., 2016). These studies often examined only a single group of birds. For example, focusing on 13 species of Anseriformes in northeastern California and western Nevada, Matthias (1963) documented 10 helminth taxa among 49 individual birds, most of which represented new host and geographic records, not surprising because it was one of the first bird-related studies on helminths in these states. Ching (1990) studied 2 species of Charadriiformes Huxley, 1867, *Calidris alpina* L., 1758 (Dunlin) and *Tringa semipalmatus* (Gmelin, 1789) (Willet), from sites in Bodega Bay and Bolinas Lagoon, identifying 17 helminth taxa. More recently, Baker et al. (1996) studied 18 bird species in northern California and found that 23% of the Falconiformes Sharpe, 1874, and 44% of the Strigiformes Wagler, 1830, were infected with intestinal parasites (Baker et al., 1996). Similarly, Hannon et al. (2016) investigated how bird species traits correlated with helminth richness among 21 bird species from the San Francisco Bay Area in California. They detected 64 helminth taxa throughout 57 individual hosts, for which parasite richness ranged from 0 to 16 different taxa among each bird species (Hannon et al., 2016). Although these studies provided valuable information on infection patterns among bird species in California, they are few in number and limited in both geographic and taxonomic scope, emphasizing the need for additional research within the state. Given that California is home to over 580 bird species, it is important to examine species that have not previously been surveyed for helminths (Dawson, 1923; Cogswell, 1977).

The protected status of many bird species emphasizes the importance of methodological approaches that do not require direct sacrifice of the host, including nonlethal sampling as well as opportunistic collections (Baus et al., 2019). Alongside noninvasive sampling methods such as fecal egg counts and eDNA (Laude et al., 2016; Lobos-Ovalle et al., 2021), opportunistic and humane salvage of dead or dying birds provides an important complementary approach because it (1) provides morphologic specimens of parasites that may be valuable for species identification and life cycle studies (Blasco-Costa and Poulin, 2017), (2) can yield specimens of parasites that are not detectable from fecal or environmental samples, including those outside of the gastrointestinal tract or not currently releasing eggs (Bensch and Hellgren, 2020; Huang et al., 2020; Thaenkham et al., 2022), and (3) offers direct and quantitative information on parasite community composition and infection load (Galbreath et al., 2019). The act of salvaging, which is using the body of euthanized or found deceased animals, is a viable way to study internal helminths because of the inability to survive on their own in the wild, even if such samples are nonrandom (McAllister et al., 2022). Collected helminth samples may also be submitted to museums and parasite-focused databases, which help to build an infrastructure on the basis of understanding the complex relationships between hosts and parasites and help elucidate the life cycle of parasites with multiple hosts (Blasco-Costa and Poulin, 2017; Galbreath et al., 2019).

In the current study, we obtained birds from wildlife organizations and groups in California over 4 yr to better describe and understand variation in helminth communities in the San Francisco Bay Area in California. Specifically, we dissected 17 species from 6 common bird orders and recorded the identities and prevalence of helminth taxa. We focused on the orders Anseriformes, Pelecaniformes Sharpe, 1891, Passeriformes L., 1758, Accipitriformes Viellot, 1816, and Suliformes Sharpe, 1891, and Galliformes Temminck, 1820, which have a wide variety of diets, such as amphibians, fish, and terrestrial organisms, and use diverse habitats, such as freshwater and marine environments. A single galliform was also included. The San Francisco Bay Area of California is positioned in the middle of the Pacific Flyway, which represents an important migratory route for hundreds of bird species (Cogswell, 1997; Reisen, 2010). Many bird species, such as herons and egrets, also use the San Francisco Bay Area of California as nesting grounds during migration (Kelly et al., 2007). By extending research on the helminths found in California birds, this study aims to shed light on patterns and presence of different parasites from multiple avian host groups from an understudied region.

MATERIALS AND METHODS

Animal collection and dissection

Bird gastrointestinal tracts were collected from wildlife rehabilitation centers (International Bird Rescue and WildCare Rescue Services), museums (California Academy of Sciences), and local hunting groups (U.S. Fish and Wildlife Service permit: MBPER0028773) from 13 counties in and around the Bay Area of California from 2019 to 2023 (Fig. 1). Following euthanasia or death, the carcasses of birds were either immediately frozen, or the gastrointestinal tract was removed before freezing in a standard freezer (−20 C). Frozen gastrointestinal tracts were sent to the University of Colorado–Boulder in ice-packed coolers overnight. Upon arrival, intestinal tracts were stored at −20 C until dissection, when they were allowed to thaw to room temperature. In most cases, except for Anseriformes Wagler, 1831 provided by hunters, the birds collected had health conditions and were euthanized but not treated with anthelmintics. As such, the collection of individuals was opportunistic and not intended as a representative or random sample of the helminth communities for each species. Nonetheless, such samples provide a valuable opportunity to gain insight into the parasite fauna for taxa that are protected or sensitive to direct harvest. All bird species were identified by the collaborators. The scientific name of each bird was retrieved from the American Ornithological Society Checklist of North and Middle American Birds databases (Chesser et al., 2024). All authorities were gathered from the International Commission on Zoological Nomenclature, the Clements Checklist of Birds of the World, and a literature review.

Bird gastrointestinal tracts were necropsied following the methods of Kinsella and Forrester (1972) and Hannon et al. (2016) following a proper training procedure. The gastrointestinal tract was dissected in the following order: esophagus, stomach, small intestine, and large intestine or ceca. Each section was divided into 2- to 5-cm segments. The tissue was teased and shredded using forceps to remove food contents and free parasites embedded in tissues. The contents of each section were rinsed with tap water into plastic gridded petri dishes, and both the contents and tissue were then examined under an Olympus SZX10 stereo-dissection microscope (Olympus Corporation, Tokyo, Japan) on a magnification range of x6.3 to x63 to detect and isolate helminths. Photos of helminths were taken on an Olympus BX51 microscope using cellSens Standard V2.2 Microscope Imaging Software (Figs. 2, 3). This procedure was repeated

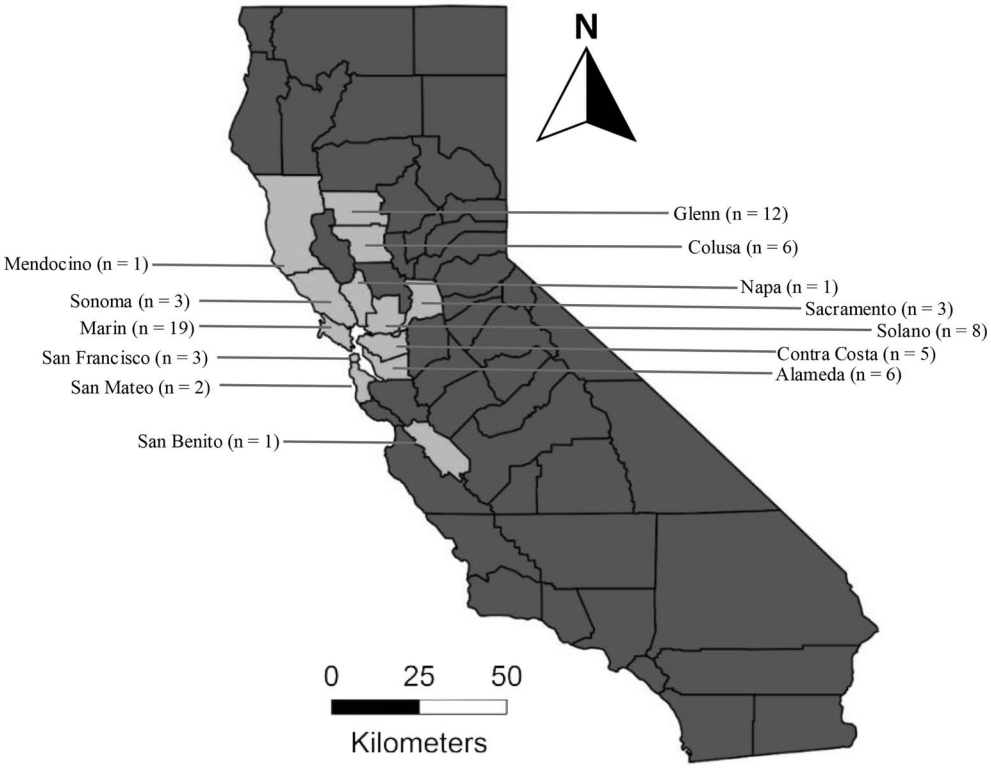

Figure 1. Map of the state of California. Counties highlighted in light grey indicate counties from which bird specimens in this project were collected from 2019 to 2023. Each county is titled and indicates the number (n) of specimens donated from each county.

for each section. Isolated parasites were quantified and preserved in 95% ethanol for molecular study (see below). The following statistical definitions follow as described by Margolis et al. (1982) and Bush et al. (1997). Prevalence was calculated by the number of individuals of a host species infected with a parasite species divided by the number of hosts examined (Margolis et al., 1982; Bush et al., 1997). The mean intensity was calculated by the total number of a particular parasite species divided by the number of infected hosts, whereas mean abundance was calculated as the total number of parasites divided by the total number of hosts (Margolis et al., 1982; Bush et al., 1997).

Parasite identification

Trematodes and cestodes were stained with Semichon's carmine or Harris hematoxylin (Sepulveda and Kinsella, 2013). In some cases, squashes of cestode rostellar hooks were made in lactophenol for more accurate measurements (Sepulveda and Kinsella, 2013). Both nematodes and acanthocephalans were cleared and examined in temporary mounts of lactophenol and then returned to 95% ethanol. To classify detected helminths on the basis of morphology, we relied on the following taxonomic keys: trematodes (Yamaguti, 1958, 1971; Gibson et al., 2002; Jones et al., 2005; Bray et al., 2008); nematodes (Yamaguti 1963a; Anderson et al., 2009); cestodes (Yamaguti, 1959; Schmidt, 1970, 1986; Khalil et al., 1994); and acanthocephalans (Yamaguti, 1963b). Whenever possible, helminths were identified to the species level using reference specimens, including those in the personal collection of author J.M.K. However, due to degradation or larval stages of some helminths, others were keyed only to genus or family.

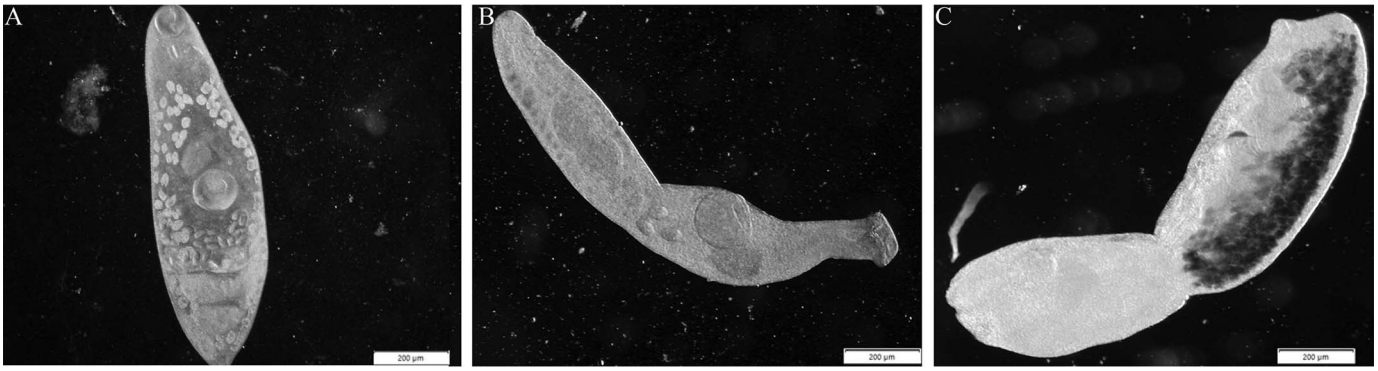

Figure 2. Microscopic images of (**A**) *Ribeiroia ondatrae* from *Nycticorax nycticorax*, (**B**) *Echinoparyphium ellisi* from *Aythya collaris*, and (**C**) *Australapatemon burti* from *Aythya collaris*.

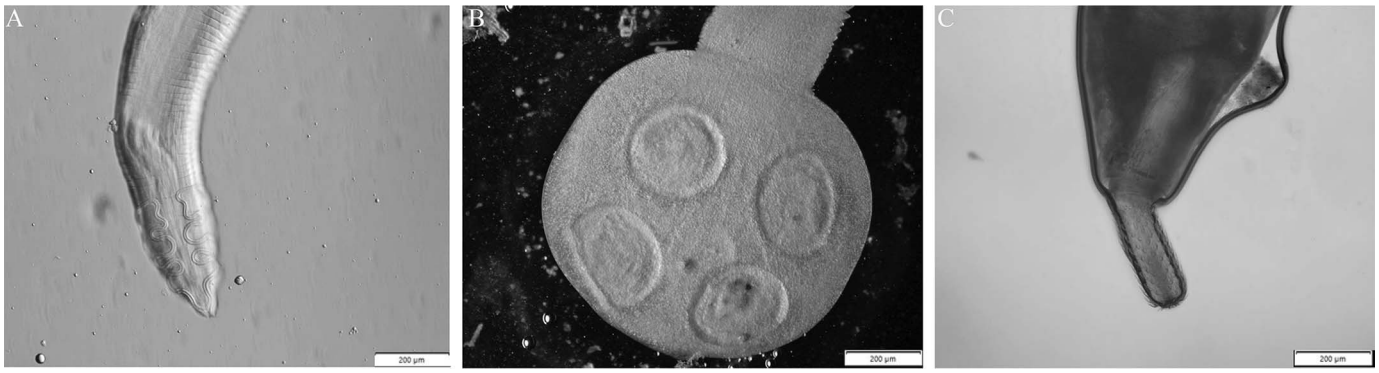

Figure 3. Microscopic images of (**A**) *Dispharynx nasuta* from *Meleagris gallopavo*, (**B**) *Cloacotaenia megalops* from *Aythya collaris*, and (**C**) *Plagiorhynchus cylindraceus* from *Corvus brachyrhynchos*.

A subset of trematodes was used for DNA sequencing. Genomic DNA was extracted from whole digeneans according to the protocol of Tkach and Pawlowski (1999). An approximately 1,300-base-pair-long fragment at the 5′ end of *28S* rDNA was amplified by polymerase chain reaction (PCR) on a T100™ Thermal Cycler (Bio-Rad, Hercules, California). PCRs were carried out using forward primer digL2 (5′–AAG CAT ATC ACT AAG CGG–3′) and reverse primer 1500R (5′–GCT ATC CTG AGG GAA ACT TCG–3′) (Tkach et al., 2003). PCRs were performed in a total volume of 25 µl using One*Taq* Quick-Load PCR mix from New England Biolabs (Ipswich, Massachusetts) according to the manufacturer's protocol. An annealing temperature of 53 C was used. PCR products were purified using an ExoSAP-IT PCR Cleanup Enzymatic Kit from Affymetrix (Santa Clara, California). PCR products were cycle sequenced using a BrightDye Terminator Cycle Sequencing Kit (MCLAB, South San Franscisco, California). Sequencing reactions were purified using a MCLab BigDye Sequencing Clean Up Kit and run on an ABI 3500 Genetic Analyzer (Thermo Fisher Scientific, Waltham, Massachusetts). Contiguous sequences were assembled using Sequencher version 5.4 software (GeneCodes Corporation, Ann Arbor, Michigan) and deposited under GenBank PV075037–PV075055 (Table I). Unfortunately, many of the trematode samples were too degraded for DNA amplification and sequencing. We were only able to generate DNA sequences of 10 species.

Table I. Hosts and GenBank numbers of digeneans sequenced in the present study.

Digenean species	Host species	GenBank nos.
Ascocotyle sp.	*Ardea alba*	PV075037
Australapatemon cf. *burti*	*Anas acuta*	PV075039
Au. cf. *burti*	*Ay. collaris*	PV075038
Clinostomum marginatum	*Ardea herodias*	PV075040, PV075041
Cotylurus sp.	*Mareca americana*	PV075042
Echinoparyphium ellisi	*Ay. collaris*	PV075043
Microphallidae gen. sp.	*Anas platyrhynchos*	PV075044–PV075046
Notocotylus sp.	*An. platyrhynchos*	PV075047
Posthodiplostomum centrarchi	*Ar. herodias*	PV075048–PV075050
Po. centrarchi	*Nycticorax nycticorax*	PV075051
Wardius lunatus	*An. acuta*	PV075053, PV075054
W. lunatus	*Ay. collaris*	PV075052
W. lunatus	*M. americana*	PV075055

RESULTS

Throughout the project, 70 birds were dissected, representing 6 orders and 17 species (Table II). Birds were collected in 2019 (n = 8), 2020 (n = 2), 2021 (n = 3), 2022 (n = 53), and 2023 (n = 4). Collectively, this included birds from 13 counties within California (Fig. 1), with Marin (n = 19) as the most sampled county. The most sampled host taxa were *Corvus brachyrhynchos* Brehm, 1822 (American crow; n = 19) and *Anas acuta* L., 1758 (Northern pintail; n = 10). The most species-rich order was Anseriformes, represented by 3 genera including 5 species (*An. acuta*, *Aythya collaris* Donovan, 1809 [ring-necked duck], *Anas platyrhynchos* L., 1758 [mallard], *Mareca strepera* L., 1758 [gadwall], and *Mareca americana* Gmelin, 1789 [American wigeon]). For nearly 71% of our specimens, sex was unknown, with the remainder primarily males (n = 18).

Bird species and individuals varied in helminth richness, species composition, and abundance. Eighty-seven percent of birds were infected with 1 or more helminths. Only 9 birds from 3 host species, *C. brachyrhynchos* (n = 5), *M. strepera* (n = 2), and *An. acuta* (n = 2), had no helminth infections. Among birds that were infected (n = 61), 86% were infected with nematodes, 36% with trematodes, 16% with cestodes, and 16% with acanthocephalans. Nematodes in infected birds were found in the stomach and esophagus (31%) and infrequently in the small intestine (26%) or large intestine (11%). Trematodes were located predominantly in the small intestine (56%) and less frequently in the large intestine and ceca (20%), esophagus (14%), or stomach (4%). Finally, both cestodes and acanthocephalans were commonly found within the small intestine (83 and 63%, respectively). However, the location of parasites within the intestinal tract can differ due to the migration of worms after host death (Sepulveda and Kinsella, 2013). The Anseriformes (n = 22) had the highest helminth richness, with a cumulative total of 18 taxa. Among individual bird species, *N. nycticorax* (black-crowned night heron; n = 9) and *Ardea herodias* (great blue heron; n = 3) supported the highest helminth richness values, with 7 identified and 1 unidentified helminth taxa.

We identified 39 helminth taxa across 70 individual specimens: 4 acanthocephalans, 5 cestodes, 15 nematodes, and 15 trematodes (Tables III–VI). Of those, 26 taxa were identified to species through morphologic analysis, molecular analysis, or both. Thirty-three of these are new geographic records, and 22 are new host records

Table II. List of birds collected in different counties of California from 2019 to 2023. The scientific name of each bird was retrieved from the Checklist of North American Birds database (Chesser et al., 2024).

Common name	Scientific name	Total no. collected	Method of collection	Collection county (no. of birds)	Years collected
Accipitriformes					
Osprey	*Pandion haliaetus*	2	Rehabilitation centers	Contra Costa (1); Solano (1)	2021; 2022
Red-tailed hawk	*Buteo jamaicensis*	1	Rehabilitation centers	San Francisco (1)	2022
Red-shouldered hawk	*Buteo lineatus*	1	Rehabilitation centers	Marin (1)	2022
Cooper's hawk	*Accipiter cooperii*	1	Rehabilitation centers	San Francisco (1)	2020
Anseriformes					
Mallard	*Anas platyrhynchos*	2	Hunting	Marin (2)	2019; 2021
American wigeon	*Mareca americana*	5	Hunting	Colusa (1); Glenn (4)	2022
Northern pintail	*Anas acuta*	10	Hunting	Colusa (2); Glenn (8)	2022
Gadwall	*Mareca strepera*	4	Hunting	Colusa (3); Sonoma (1)	2022
Ring-necked duck	*Aythya collaris*	1	Hunting	Sonoma (1)	2023
Galliformes					
Wild turkey	*Meleagris gallopavo*	1	Hunting	Sonoma (1)	2022
Passeriformes					
American crow	*Corvus brachyrhynchos*	19	Hunting	Alameda (1); Contra Costa (2); Marin (13); San Francisco (1); San Mateo (2)	2019; 2022
Red-winged blackbird	*Agelaius phoeniceus*	1	Rehabilitation centers	Marin (1)	2022
Pelecaniformes					
Black crowned night heron	*Nycticorax nycticorax*	9	Rehabilitation centers	Alameda (4); Contra Costa (1); Sacramento (3); Solano (1)	2022
Snowy egret	*Egretta thula*	7	Rehabilitation centers	Alameda (1); Solano (6)	2022
Great blue heron	*Ardea herodias*	3	Rehabilitation centers	Marin (1); Mendocino (1); Napa (1)	2020; 2021; 2022
Great egret	*Ardea alba*	2	Rehabilitation centers	Contra Costa (1); San Benito (1)	2019; 2022
Suliformes					
Double-crested cormorant	*Nannopterum auritum*	1	Rehabilitation centers	Marin (1)	2022

Table III. Endohelminths collected from pelecaniforms. The scientific name of each bird was retrieved from the Checklist of North American Birds database (Chesser et al., 2024).

	Nycticorax nycticorax (n = 9)*		*Egretta thula* (n = 7)		*Ardea herodias* (n = 3)		*Ardea alba* (n = 2)	
Helminth taxa	P†	I‡	P	I	P	I	P	I
Acanthocephala								
Polymorphus brevis	22.2	7.0 (0–18)	–	–	33.3	1.0 (0–1)	–	–
Cestoda								
Dendrouterina nycticoracis	22.2	5.3 (0–13)	–	–	–	–	–	–
Nematoda								
Contracaecum multipapillatum	88.9	23.7 (0–310)	–	–	66.7	21.7 (0–61)	–	–
Contracaecum sp.	–§	–	71.4	5.5 (0–20)	33.3	6.0 (0–14)	50.0	2.5 (0–3)
Desmidocercella numidica	–	–	–	–	66.7	1.0 (0–1)	50.0	1.0 (0–1)
Desportesius invaginatus	–	–	85.7	3.0 (0–9)	–	–	50.0	13.0 (0–13)
Trematoda								
Ascocotyle sp.	33.3	1.3 (0–2)	57.1	77.4 (0–366)	–	–	50.0	10.0 (0–10)
Clinostomum sp.	11.1	7.0 (0–7)	14.3	1.0 (0–1)	–	–	–	–
Clinostomum marginatum	–	–	–	–	33.3	2.5 (0–4)	–	–
Posthodiplostomum centrarchi	33.3	25.4 (0–67)	–	–	33.3	23.7 (0–89)	–	–
Posthodiplostomum sp.	–	–	28.6	2.7 (0–6)	33.3	66.7 (0–156)	50.0	2.0 (0–2)
Ribeiroia ondatrae	11.1	2.0 (0–2)	–	–	–	–	–	–
Unidentified echinostomatid	–	–	71.4	5.5 (0–36)	–	–	–	–
Unidentified trematode	22.2	2.0 (0–3)	14.3	6.8 (0–13)	–	–	–	–

* n = The host sample size (number of birds dissected).
† P = Prevalence: the number of individuals of a host species infected with a parasite species divided by the number of hosts examined presented as a percentage.
‡ I = Mean intensity followed by range in parentheses: the total number of individuals of the parasite species divided by the number of infected host individuals and the range of helminths (in parentheses).
§ Dash (–) = This helminth was not recorded in this host.

(Table VII). The remaining 13 taxa were identified to genus or family. Of the helminths we identified to species, *Contracaecum multipapillatum* (Von Drasche, 1882) was found across 3 host species (*Ar. herodias*, *N. nycticorax*, and *Pandion haliaetus* L., 1758 [osprey]). We saw overlap in 2 other nematode taxa, *Desportesius invaginatus* (Linstow, 1901), with *Egretta thula* (Molina, 1782) (snowy egret), and *Ardea alba* L., 1758 (great egret), and *Desmidocercella numidica* Seurat, 1920 (*Ar. herodias* and *Ar. alba*), which occurred exclusively

Table IV. Endohelminths collected from accipitriforms. The scientific name of each bird was retrieved from the Checklist of North American Birds database (Chesser et al., 2024).

	Pandion haliaetus (n = 2)*		*Buteo jamaicensis* (n = 1)		*Buteo lineatus* (n = 1)		*Accipiter cooperii* (n = 2)	
Helminth taxa	P†	I‡	P	I	P	I	P	I
Nematoda								
Capillaria falconis	–§	–	–	–	–	–	100.0	9.3 (4–13)
Contracaecum multipapillatum	100.0	25.5 (1–118)	–	–	100.0	2.5 (1–4)	–	–
Synhimantus laticeps	–	–	100.0	7.7 (1–19)	–	–	–	–
Trematoda								
Galactosomum sp.	50.0	5.0 (0–5)	–	–	–	–	–	–

* n = The host sample size (number of birds dissected).
† P = Prevalence: the number of individuals of a host species infected with a parasite species divided by the number of hosts examined presented as a percentage.
‡ I = Mean intensity followed by range in parentheses: the total number of individuals of the parasite species divided by the number of infected host individuals and the range of helminths (in parentheses).
§ Dash (–) = This helminth was not recorded in this host.

Table V. Endohelminths collected from anseriforms. The scientific name of each bird was retrieved from the Checklist of North American Birds database (Chesser et al., 2024).

	Anas acuta (n = 10)*		*Anas platyrhynchos* (n = 2)		*Aythya collaris* (n = 1)		*Mareca americana* (n = 5)		*Mareca strepera* (n = 4)	
Helminth taxa	P†	I‡	P	I	P	I	P	I	P	I
Acanthocephala										
Corynosoma constrictum	–§	–	50.0	10.0 (0–10)	–	–	–	–	–	–
Cestoda										
Cloacotaenia megalops	–	–	–	–	100.0	1.0	–	–	–	–
Diorchis sp.	–	–	–	–	–	–	40.0	1.5 (0–2)	–	–
Hymenolepis hopkinsi	–	–	50.0	1.0 (0–1.0)	–	–	–	–	–	–
Unidentified cestode	10.0	1.0 (0–1)	–	–	100.0	1.0	20.0	1.0 (0–1)	25.0	1.0 (0–1)
Nematoda										
Amidostomum acutum	–	–	–	–	–	–	20.0	1.0 (0–1)	–	–
Capillaria sp.	10.0	5.0 (0–5)	–	–	–	–	20.0	1.0 (0–1)	–	–
Contracaecum sp.	–	–	50.0	3.0 (0–5)	–	–	–	–	25.0	5.0 (0–5)
Epomidiostomum uncinatum	–	–	–	–	–	–	40.0	2.5 (0–4)		
Tetrameres sp.	20.0	5.5 (0–9)	–	–	–	–	–	–	–	–
Unidentified nematode	–	–	–	–	100.0	1.0 (1)	–	–	–	–
Trematoda										
Australapatemon cf. *burti*	10.0	2.0 (0–2)			100.0	4.0				
Clinostomum sp.			50.0	5.5 (0–10)						
Cotylurus sp.							20.0	1.0 (0–1)		
Echinoparyphium recurvatum			50.0	68.0 (0–68)						
Echinoparyphium ellisi					100.0	55				
Notocotylus sp.	10.0	1.0 (0–1)	50.0	283.0 (0–283)						
Wardius lunatus	40.0	1.0 (0–1)			100.0	3.0	40.0	1.0 (0–1)		
Unidentified echinostomatid	10.0	1.0 (0–1)			–	–				
Unidentified microphallid			100.0	96.7 (10–267)						
Unidentified trematode			50.0	1.0 (0–1)	100.0	3.0				

* n = The host sample size (number of birds dissected).
† P = Prevalence: the number of individuals of a host species infected with a parasite species divided by the number of hosts examined presented as a percentage.
‡ I = Mean intensity followed by range in parentheses: the total number of individuals of the parasite species divided by the number of infected host individuals and the range of helminths (in parentheses).
§ Dash (–) = This helminth was not recorded in this host.

among hosts in the pelecaniforms. The acanthocephalan *Polymorphus brevis* Van Cleave, 1916, was found in both *Ar. herodias* and *N. nycticorax*. No cestodes were found to occur in multiple host species.

For helminths identified only to genus, multiple taxa overlapped within the examined host species. The nematode genus *Contracaecum* Railliet and Henry, 1912, was found in 6 different host species (*Ar. herodias*, *E. thula, Ar. alba, Buteo lineatus* Gmelin, 1788 [red-shouldered hawk], *An. platyrhynchos*, and *M. strepera*). Among the trematodes, there were 3 genera found across multiple host species: *Clinostomum* Leidy, 1856; *Posthodiplostomum* Dubois, 1936; and *Wardius* Barker and East, 1915. *Clinostomum* specimens were found in 3 bird species (*N. nycticorax*, *An. platyrhynchos*, and *E. thula*). Members of *Posthodiplostomum* were found in 4 different bird species (*Ar. herodias*, *Ar. alba*, *E. thula*, *N. nycticorax*). Finally, the trematode *Wardius lunatas*

Table VI. Endohelminths collected from suliforms, passeriforms, and a galliform. The scientific name of each bird was retrieved from the Checklist of North American Birds database (Chesser et al., 2024).

	Agelaius phoeniceus (n = 1)*		*Corvus brachyrhynchos* (n = 19)		*Meleagris gallopavo* (n = 1)		*Nannopterum auritum* (n = 1)	
Helminth taxa	P†	I‡	P	I	P	I	P	I
Acanthocephala								
Mediorhynchus sp.	100.0	1.0	–	–	–	–	–	–
Plagiorhynchus cylindraceus	–§	–	21.1	4.25 (0–14)	–	–	–	–
Cestoda								
Metroliasthes lucida	–	–	–	–	100.0	13.0	–	–
Nematoda								
Capillaria corvorum	–	–	47.4	74.5 (0–503)				
Cosmocephalus obvelata	–	–	–	–	–	–	100.0	45.7
Dispharynx nasuta	–	–	–	–	100.0	1.0	–	–
Eucoleus contortus	–	–	57.9	196.9 (0–1,606)	–	–	–	–

* n = The host sample size (number of birds dissected).
† P = Prevalence: the number of individuals of a host species infected with a parasite species divided by the number of hosts examined presented as a percentage.
‡ I = Mean intensity followed by range in parentheses: the total number of individuals of the parasite species divided by the number of infected host individuals, and the range of helminths (in parentheses).
§ Dash (–) = This helminth was not recorded in this host.

(Diesing, 1836) was found in 3 duck species (*M. americana*, *An. acuta*, and *Ay. collaris*). Because of the degradation of samples, 1 cestode, 5 trematodes, and 1 nematode were considered "unknown" and could represent additional species.

Similar to richness, average helminth abundance and intensity (see Tables III–VI for intensity) varied across hosts and helminth taxa. Nematodes were the most abundant group across all hosts, with an average ± 1 SE abundance of 75.1 ± 23.7 (range: 1 to 1,606). The most abundant nematode was *Eucoleus contortus* (Rudolphi, 1819), which was found in *C. brachyrhynchos* and had a maximum abundance of 1,606 in a single crow and an average ± 1 SE abundance of 214.5 ± 101 across 19 specimens. Trematodes were the next most abundant helminths. *Ascocotyle* sp. had the highest maximum abundance of 366, with an average ± 1 SE abundance of 25.1 ± 28.4, followed closely by *Posthodiplostomum* members, with a maximum abundance of 156 and an average ± 1 SE abundance of 19.2 ± 10.5. Acanthocephalans and cestodes both supported lower abundances than nematodes and trematodes. The highest abundance for acanthocephalans was for *P. brevis*, found in the hosts *N. nycticorax* and *Ar. herodias*, with a maximum abundance of 18 in a single bird and an average abundance of 2.5 ± 1.8 SE. Finally, the cestode taxon, *Dendrouterina nycticoracis* Olsen, 1937, had a maximum abundance of 13 and an average of 1.7 ± 1.8 SE.

The newly generated *28S* sequences were compared with those available in GenBank using BLAST. As a result, we were able to confirm the identities of 10 digenean species. All nominal species were 100% matches to sequences previously available in GenBank. Three of these species were from ardeids, including the detection of *Ascocotyle* sp. (Heterophyidae Leiper, 1909) from *Ar. alba*, *Clinostomum marginatum* (Rudolphi, 1819) (Clinostomidae Lühe, 1901) from *Ar. herodias*, and *Posthodiplostomum centrarchi* Hoffman, 1958 (Diplostomidae Poirier, 1886) from both *Ar. herodias* and *N. nycticora*x. The other 7 species were sequenced from anatids: *Australapatemon* cf. *burti* (Diplostomidae) from *Ay. collaris* and *An. acuta*; *Cotylurus* sp. (Diplostomidae) from *M. americana*; and *Echinoparyphium ellisi* (Johnston and Simpson, 1944) (Echinostomatidae Looss, 1899) from *Ay. collaris*. The 2 microphallidae spp. and *Notocotylus* sp. (Notocotylidae Lühe, 1909) were both sequenced from *An. platyrhynchos*. Finally, *W. lunatus* was sequenced from *Ay. collaris*.

DISCUSSION

By examining opportunistically collected birds representing 17 species from California, this study provided insight into the diversity of helminths in birds from a region with relatively few previous parasitologic surveys. The combination of both molecular and morphologic examination facilitated identification of 39 helminth taxa, including: 4 acanthocephalans, 5 cestodes, 15 nematodes, and 15 trematodes. An additional 9 helminth taxa were unidentified due to the degradation of samples. Twenty-eight parasite taxa were identified to species, and the remainder were identified to genus. To the best of our knowledge, 33 of these records represent new geographic records of helminths found within the state of California. Our study identified new host–parasite records that have not been documented previously in the United States, such as the detection of the trematode *Ribeiroia ondatrae* in *N. nycticorax* and 21 other helminths from other bird hosts.

Our results indicated a high richness and abundance of helminth taxa compared with previous studies conducted in California. In total, we examined 17 different bird species, some of which had been included in previous helminth surveys (Ching, 1990; Baker et al., 1996; Hannon et al., 2016) and documented 33 helminth taxa not previously reported from California. In a study focused on 2 charadriiforms, *C. alpina* and *T. semipalmatus*, Ching (1990) found 17 helminth taxa across 34 birds but with no overlap with the parasites reported in this study. We also found little overlap with the helminths reported by Baker et al. (1996) in a study of 4 species of Falconiformes and Strigiformes in California. Even among avian taxa examined in both studies (e.g., *Accipiter cooperii* Bonaparte, 1928 [Cooper's hawk], *B. lineatus*, *Buteo jamaicensis* Gmelin, 1788 [red-tailed hawk]), none of the 4 reported helminths in the study was detected within our survey (*Capillaria* sp., *Co. multipapillatum*, *Synhimantus laticeps* [Rudolphi, 1819], and *Galactosomum* sp. Looss, 1899). This was likely because Baker et al. (1996) used only fecal samples to detect infections. Our study

Table VII. Geographic and host records for endohelminths found in bird species collected in California. Due to the postmortem status of the hosts, where the parasite was found does not represent definitive locations. Seventy individual birds were examined that represented 17 species of birds from 6 orders.

Helminth taxa	No. of birds infected	Bird host species	Location in host*
Acanthocephala			
Mediorhynchus sp.	1	*Agelaius phoeniceus*	SI
Plagiorhynchus cylindraceus	4	*Corvus brachyrhynchos*†	S, SI
Polymorphus brevis	1	*Ardea herodias*	SI
Cestoda			
Cloacotaenia megalops	1	*Aythya collaris*†	S
Dendrouterina nycticoracis	2	*Nycticorax nycticorax*	SI
Diorchis sp.	2	*Mareca americana*†	C, LI, SI
Hymenolepis hopkinsi	1	*Anas platyrhynchos*	C, LI
Metroliasthes lucida	1	*Meleagris gallopavo*	SI
Nematoda			
Amidostomum acutum	1	*M. americana*†	S
Capillaria corvorum	9	*C. brachyrhynchos*†	C, LI, SI
Capillaria falconis	1	*Accipiter cooperii*†	C, S, SI, LI
Capillaria sp.	1	*M. americana*†	C, LI
Contracaecum multipapillatum	2	*Ar. herodias*	E, S, SI
Co. multipapillatum	8	*N. nycticorax*	C, E, S, LI, SI
Co. multipapillatum	2	*Pandion haliaetus*	E, S, SI
Co. multipapillatum	1	*Buteo lineatus*	E, S
Contracaecum sp.	5	*Egretta thula*	E, SI
Contracaecum sp.	1	*Ardea alba*†	SI
Contracaecum sp.	1	*Anas platyrhynchos*†	E, S
Contracaecum sp.	1	*Mareca strepera*†	E
Cosmocephalus obvelata	1	*Nannopterum auritum*†	E, S, SI
Desportesius invaginatus	6	*E. thula*†	S
Dispharynx nasuta	1	*Me. gallopavo*	E
Epomidiostomum uncinatum	2	*M. americana*	S
Eucoleus contortus	11	*C. brachyrhynchos*	E, S
Synhimantus laticeps	1	*Buteo jamaicensis*†	S, SI
Tetrameres sp.	2	*Anas acuta*	S
Trematoda			
Ascocotyle sp.	1	*Ar. alba*	SI
Australapatemon cf. *burti*	1	*Ay. collaris*†	SI
Clinostomum marginatum	1	*Ar. herodias*	E
Clinostomum sp.	1	*N. nycticorax*	E
Clinostomum sp.	1	*E. thula*†	C, LI
Clinostomum sp.	1	*An. platyrhynchos*†	C, LI, SI
Cotylurus sp.	1	*M. americana*†	SI
Echinoparyphium ellisi	1	*Ay. collaris*†	E, SI
Echinoparyphium recurvatum	1	*An. platyrhynchos*	SI
Galactosomum sp.	1	*Pa. haliaetus*	SI
Posthodiplostomum centrarchi	2	*Ar. herodias*	E, SI
Po. centrarchi		*N. nycticorax*†	SI
Posthodiplostomum sp.	2	*E. thula*	SI
Posthodiplostomum sp.	1	*Ar. alba*	S
Notocotylus sp.	1	*An. platyrhynchos*†	C, LI
Notocotylus sp.	1	*An. acuta*†	C, LI
Ribeiroia ondatrae	1	*N. nycticorax*†	S
Wardius lunatus	1	*M. americana*	C, LI
W. lunatus	4	*An. acuta*	C, LI
W. lunatus	1	*Ay. collaris*†	C, LI

* Abbreviations for location in host: C = ceca; E = esophagus; LI = large intestine; S = stomach; SI = small intestine.
† New host or geographic records or both.

had the most overlapping helminth taxa (n = 12) with the survey reported by Hannon et al. (2016). In comparison to our study, Hannon et al. (2016) found a greater overall helminth richness, with 5 acanthocephalans, 8 cestodes, 24 nematodes, and 27 trematodes. An interesting contrast between the 2 studies involved the intensity of infection between parasites encountered. For instance, *D. invaginatus* was present in *Ar. alba* from both studies, but the current study reported a higher average intensity of 13.0 compared with 2.0 (Hannon et al., 2016). Similarly, *P. brevis* was found in *N. nycticorax* from both studies' hosts, but with a lower prevalence in the current study (22% of 9 hosts) relative to Hannon et al. (2016) (50% of 4 hosts). Differences in average intensity and prevalence are likely due to differences in the quantity, age, and specific collection locations for each host species.

The differences in richness and intensity of helminth infections between our study and previous surveys in California are likely due to variation in sample size, host species examined, seasonality, and intrinsic host traits. Although there were several helminth taxa

in common, such as *P. brevis*, *D. invaginatus*, *Ascocotyle* sp., and *Clinostomum* sp., Hannon and colleagues (2016) reported more helminth diversity than was observed here. Potential reasons for this difference include differences in the number of avian species examined (21 vs. 17) and variation in the identities of species examined (our study did not examine *Butorides virescens* [L., 1758] [green heron], *Podilymbus podiceps* [L., 1758] [pied-billed grebe], or *Bucephala albeola* [L., 1758] [bufflehead], for example). Many of the hosts sampled by Hannon et al. (2016) are known to have a wide diversity of helminths, which could explain the differences in richness detected between the 2 studies (Stock and Holmes, 1988; Sitko and Heneberg, 2015). Intrinsic host traits, such as diet, are often closely linked to parasite diversity and infection prevalence in vertebrate hosts (Kennedy et al., 1986; Sanmartín et al., 2004). For instance, Hannon and colleagues (2016) determined that sampled carnivorous birds supported 30% greater helminth richness than birds considered predominantly herbivorous. Even the season and timing of bird collection can affect the community of parasites infecting a host (Davidson et al., 1980; Senlik et al., 2005; Naphade and Chaudhari, 2013). In a project on the seasonal trends of quail parasites, Davidson and colleagues (1980) determined that several parasite species peaked in abundance during the summer months and decreased dramatically during winter. Given that our sampling and collection were opportunistic and nonrandom, relying heavily on the specimen availability from collaborators in California, birds included in this study were not able to be stratified in collection through seasons. All these factors have the potential to affect a host's parasite richness, which likely contributed to observed differences in helminth richness compared with prior studies.

The current study also reported new geographic and host records for specific helminth taxa, including the trematode *R. ondatrae*. We identified a new host record for *R. ondatrae* in the United States (*N. nycticorax*). The abundance of *R. ondatrae* was low compared with other trematodes found in *N. nycticorax*, with a total count of only 2 adult specimens within the infected bird. *Ribeiroia ondatrae* was not detected within the 8 other *N. nycticorax* specimens or any other bird species from this study. The abundance of *R. ondatrae* in this study is similar to prior host reports, as Hannon et al. (2016) and Dubois and Mahon (1959) reported an intensity of 4.0 in an *An. platyrhynchos* and 6.0 in a *Nannopterum auritum* (Lesson, 1831) (double-crested cormorant), respectively. We did not observe any *R. ondatrae* infections within the intestinal tracts of 2 *An. platyrhynchos* and 1 *N. auritum* included in the current survey. This trematode is well-documented across the United States and in a wide range of bird species known to eat fish or amphibians (see Johnson et al., 2004), such as *Ar. alba* in Florida (Sepulveda et al., 1999), *Pa. haliaetus* in Florida and Wisconsin (Kinsella et al., 1996), and *Aix sponsa* (L., 1758) (wood duck) across the Atlantic Flyway (Thul et al., 1985). Nonetheless, records of this parasite within birds remain relatively rare in California and the western United States, particularly in light of the frequent infection records among amphibian species from this region (see Johnson et al., 1999, 2001, 2013, 2023; Lunde et al., 2012).

This study advances knowledge of helminth richness within common bird species found in a relatively understudied region using a low-impact, opportunistic collection approach. By examining the helminth community in multiple bird species that vary in diet, taxonomy, and habitat use, we built upon previous research in California and documented several new geographic and host records. Our combination of morphologic and molecular techniques to characterize helminths facilitated the identification of 39 helminth taxa, helping to underscore the value of continued surveys to further understand the ecologic dynamics, geographic distribution, and life cycle biology of avian helminths.

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