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Author(s): Emily R. Hannon , John M. Kinsella , Dana M. Calhoun , Maxwell B. Joseph , and Pieter T. J. Johnson

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ENDOHELMINTHS IN BIRD HOSTS FROM NORTHERN CALIFORNIA AND AN ANALYSIS OF THE ROLE OF LIFE HISTORY TRAITS ON PARASITE RICHNESS

Emily R. Hannon, John M. Kinsella*, Dana M. Calhoun, Maxwell B. Joseph, and Pieter T. J. Johnson

Department of Ecology and Evolutionary Biology, University of Colorado, Ramaley N122 CB334, Boulder, Colorado 80309. Correspondence should be sent to: Hannon.Emily.r@gmail.com

ABSTRACT: The life history characteristics of hosts often influence patterns of parasite infection either by affecting the likelihood of parasite exposure or the probability of infection after exposure. In birds, migratory behavior has been suggested to affect both the composition and abundance of parasites within a host, although whether migratory birds have more or fewer parasites is unclear. To help address these knowledge gaps, we collaborated with airports, animal rescue/rehabilitation centers, and hunter check stations in the San Francisco Bay Area of California to collect 57 raptors, egrets, herons, ducks, and other waterfowl for parasitological analysis. After dissections of the gastrointestinal tract of each host, we identified 64 taxa of parasites: 5 acanthocephalans, 24 nematodes, 8 cestodes, and 27 trematodes. We then used a generalized linear mixed model to determine how life history traits influenced parasite richness among bird hosts, while controlling for host phylogeny. Parasite richness was greater in birds that were migratory with larger clutch sizes and lower in birds that were herbivorous. The effects of clutch size and diet are consistent with previous studies and have been linked to immune function and parasite exposure, respectively, whereas the effect of migration supports the hypothesis of “migratory exposure” rather than that of “migratory escape.”

Host traits are often associated with both the composition and diversity of parasites found in a given species. In a recent meta-analysis, Kamiya et al. (2014) found that host body size, geographic range size, and population density had consistently positive effects on the parasite richness documented across a wide range of host taxa, including plants, animals, and fungi. Such characteristics can influence infection through at least 3 mechanisms: by affecting the probability a host is exposed to parasites (e.g., larger bodied and longer lived hosts are more likely to encounter infection, Kamiya et al., 2014), by altering the likelihood they become infected after exposure, and by influencing the persistence of parasites after establishment (Agnew et al., 2000). For example, the diet of a host can alter the probability of exposure to parasites because many parasites are trophically transmitted. In a study of 6 raptor species, Santoro et al. (2012) found that the more diverse a species’ diet, the richer their parasite community. Furthermore, ecoimmunological theory suggests there are trade-offs associated with life history traits that can affect the immune system, and thus the ability for parasites to infect and persist within a host (Ricklefs and Wikelski, 2002; Johnson et al., 2012). For example, Johnson et al. (2012) showed that frogs with a faster pace of life (faster development, smaller body size, and shorter lifespan) were more susceptible to infection and pathology relative to large-bodied and slow-developing hosts. Morand and Harvey (2000) argued that mammals with longer life spans have fewer parasites, further supporting the hypothesis that infection risk could be altered by a host’s life history traits.

Among birds, migratory behavior has the potential to influence both a host’s exposure to parasites as well as the capacity of those parasites—once established—to persist (Loehle, 1995; Waldenstrom et al., 2002; Hoye, 2011). A migratory bird might have more parasites than a nonmigratory bird because they are exposed to more parasites during their passage, herein referred to as “migratory exposure.” For example, Waldenstrom et al. (2002) suggested that increases in blood parasites in migratory songbirds is a cost of migration

associated with exposure to reservoir hosts in their wintering habitats in Africa. They reported no difference in blood parasite prevalence between juveniles and adults in the resident host species of *Acrocephalus* compared to a 45% difference in prevalence between the juveniles (birds that have not migrated) and adults (after migration) in the migratory species of *Acrocephalus*. However, there is a competing hypothesis termed “migratory escape” that suggests that migration reduces either hosts’ exposure to parasites or their persistence within hosts because sources of infection, such as feces, are less likely to accumulate within a habitat and infections may be lost along their migratory path (Loehle, 1995). For example, the intensity of warble fly larva in reindeer was negatively correlated with the distance between calving grounds where larval shedding occurs and the summer pastures where transmission happens (Folstad et al., 1991). In addition, heavily infected hosts may not leave for migration at the same time as healthy hosts, thus causing a temporal separation between infective animals and noninfective animals (Hoye, 2011). These 2 opposing ideas are currently in debate (Altizer et al., 2011; Bauer and Hoye, 2014).

In the current study, we assessed the helminth diversity of raptors, egrets, herons, ducks, and other waterfowl from sites within the San Francisco Bay Area of California (hereafter Bay Area). This area is part of the Pacific Flyway, 1 of the 4 major flyways in North America, and has few previous parasitological studies of birds. We further explored the effects of bird species life history traits on parasite richness, including the influence of migratory status, while explicitly accounting for the phylogenetic relationships among host species.

MATERIALS AND METHODS

Study system

The Bay Area is located on the Pacific Flyway, the westernmost migratory route in North America that extends from Alaska into Mexico (Wilson, 2010). The Bay Area is the largest bay along the western coast, and it is where the Sacramento and San Joaquin rivers enter the Pacific Ocean (Conomos et al., 1985). This area offers a multitude of wetlands, both marine and freshwater, that offer diverse habitats for birds (Conomos et al., 1985). The Bay Area is also one of the most important sections of the Pacific Flyway as it serves as the breeding grounds, wintering grounds, or rest stops for waterfowl, shorebirds, and landbirds; millions of birds visit or live in this area (Cormier and Pitkin, 2008;

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* HelmWest Laboratory, 2108 Hilda Avenue, Missoula, Montana, 59801.

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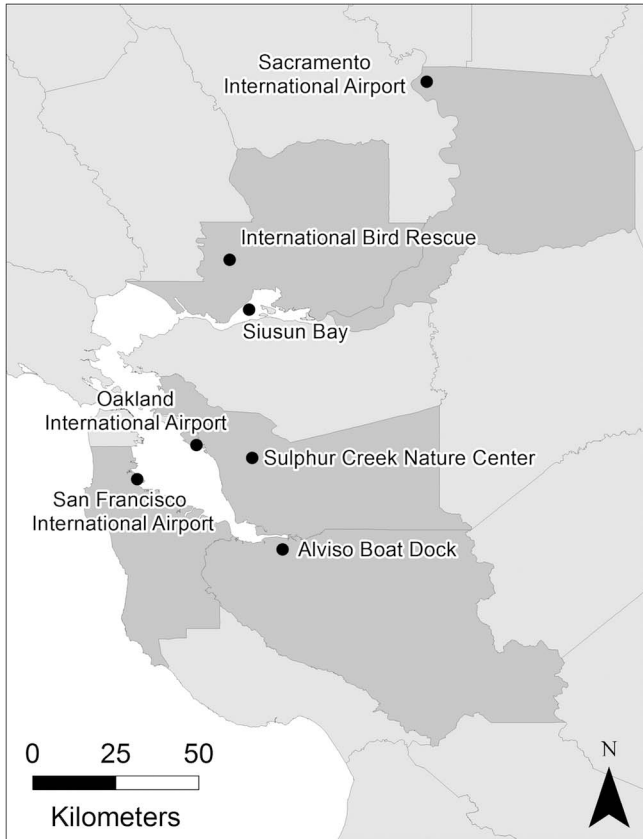


FIGURE 1. Map of bird collection sites in Bay Area of California during 2012–2013. All sites are shown as black dots.

Wilson, 2010). The combination of wetland habitats and high bird density in this area provides an opportunity for the transmission of many helminths that infect birds.

Specimen collection and species identification

To obtain samples of birds, we collaborated with Oakland International Airport, San Francisco International Airport, Sacramento International Airport, Sulphur Creek Nature Center, International Bird Rescue, and 2 hunting locations in the National Wildlife Refuge system—Alviso Boat Dock and Suisun Bay—between May 2012 and January 2013 (Fig. 1). Airports often have depredation permits that allow them to cull any birds that are a danger to planes during takeoff, which allowed us to obtain specimens. Bird rescue/rehabilitation centers provided birds that were unsuccessful rescues. At the hunting locations, we asked hunters to remove the gastrointestinal tracts from any captured animals.

After collections, birds or their gastrointestinal tracts were shipped in ice-packed coolers to the University of Colorado–Boulder, where they were stored at $-20\text{ }^{\circ}\text{C}$ until dissection and parasitological examination. Dissection and parasite identification techniques were similar to those described in Sepulveda and Kinsella (2013). The gastrointestinal tract of each bird was examined for helminths by separating the esophagus, proventriculus, gizzard, stomach, duodenum, jejunum, and ileum. Contents of each section were washed into a petri dish for examination, and then the mucosa was examined for attached parasites. The lining of the gizzard was removed and inspected and the proventriculus was teased apart to find parasites inside the glands. All of the contents of the gut were washed through a $200\text{-}\mu\text{m}$ mesh sieve followed by a $50\text{-}\mu\text{m}$ sieve, and the contents remaining on both the sieves were examined for parasites by using an SZX10 stereo-dissection microscope (Olympus Corporation, Tokyo, Japan).

Detected parasites were preserved in an alcohol–formalin–acetic acid mixture, 70% ethanol, or 95% ethanol, depending on intended use. To facilitate morphological species identification, Semichon's carmine or

Mayer's hematoxylin were used to stain trematodes and cestodes followed by mounting in Canada balsam. Nematodes were cleared in temporary mounts of lactophenol. Available literature and dichotomous identification keys were used for species identification: we used Yamaguti (1961) and Anderson et al. (2009) for the Nematoda; Yamaguti (1958, 1971), Schell (1985), Gibson et al. (2002), Jones et al. (2005), and Bray et al. (2008) for the Trematoda; Yamaguti (1963) for the Acanthocephala; and Yamaguti (1959), Schmidt (1986), and Khalil et al. (1994) for the Cestoda. Wherever possible, identification to the species level was achieved, but owing to the freezing–thawing process, higher taxonomic level identifications were often used. Voucher specimens were submitted to the Harold W. Manter Collection at the University of Nebraska–Lincoln.

Statistical analysis of life history traits

To explore and identify factors contributing to observed differences among bird species in their parasite community composition and parasite richness, we compiled a list of life history and demographic traits for each species by using data published in the literature (Craighead and Craighead, 1956; Bellrose, 1980; Hom, 1983; Rodewald, 2015). Traits that were included in our analysis included maximum longevity (years), migratory status (nonmigratory vs. migratory), maximum body mass (grams), mean clutch size (average number of eggs in a reproductive bout), and dietary preferences (predominantly herbivorous vs. carnivorous). Based on the literature, we expected that larger bodied birds would have more parasite species owing to greater exposure (Cooper et al., 2012), carnivorous birds would host a wider range of parasites due to trophic transmission, and mean clutch size would be positively associated with parasite richness due to the allocation of resources into reproduction rather than defense (Agnew et al., 2000). Migratory birds could host higher or lower parasite diversity depending on the relative effects of migratory escape versus migratory exposure (Loehle, 1995; Waldenstrom et al., 2002). For the response variable, parasite family richness was chosen instead of parasite species richness because the taxonomic resolution at the species level was inconsistent.

We developed 3 models to understand how host traits, taxonomy, and phylogeny explained parasite richness. We treated parasite richness as a Poisson distributed random variable, and modeled the expected parasite richness as a function of host clutch size, migratory status, and diet preference. These traits were chosen as explanatory variables after an initial check for collinearity among traits and graphical comparisons. The hybrid duck and Clark's grebe were excluded due to insufficient trait data. Our first and simplest model included these 3 predictors and an intercept term as parameters. The second model included the 3 predictors and intercepts that varied among species, normally distributed around zero with among-species variance estimated from the data (i.e., a species-level random effect). This model explicitly accounts for variation among host species that is unrelated to the traits that we included as covariates. A third model included the same 3 traits and induced Brownian phylogenetic correlation in the species-specific intercepts, integrating over phylogenetic uncertainty, so that closely related species may be more similar in their parasite richness than distantly related species (de Villemereuil et al., 2012). We used a posterior sample of 1,000 phylogenetic trees from birdtree.org (Jetz et al., 2012) and set a uniform prior over the distribution of correlation matrices generated from these trees to account for uncertainty in relationships among species. Priors for other parameters were also not informative. We did not include any interactions or multiplicative effects due to our small sample size and a lack of a priori-hypothesized interactions.

Support for each model was evaluated via approximate leave-one-out cross-validation with Pareto smoothed importance sampling, a Bayesian approximation for out of sample (e.g., new host species) predictive power, implemented in the "loo" R package (Gelman et al., 2014; Vehtari and Gelman, 2015). We use the posterior expected log predictive density (elpd_{100}) as a basis for model comparison. This quantity approximates a model's ability to predict future observations. Models that are well supported will have higher elpd_{100} than poorly supported models. Parameters were estimated using Markov chain Monte Carlo sampling in JAGS and R version 3.2.2 (R Development Core Team, 2015), with 3 chains for each model, and convergence was assessed with visual inspection and the R hat statistic (Plummer, 2003).

TABLE I. List of bird hosts dissected during 2012–2013.

Common name	Scientific name	Host family	Location(s)*	N (total)
Hérons and egrets				
Black crowned night heron	<i>Nycticorax nycticorax</i>	Ardeidae	SFO, IBR	4
Great blue heron	<i>Ardea herodias</i>	Ardeidae	SCR, OAK	3
Great egret	<i>Ardea alba</i>	Ardeidae	SCR, OAK	4
Green heron	<i>Butorides virescens</i>	Ardeidae	IBR	3
Snowy egret	<i>Egretta thula</i>	Ardeidae	SCN, OAK	5
Ducks, grebes and coots				
American coot	<i>Fulica americana</i>	Rallidae	SCN	1
Clark's grebe	<i>Aechmophorus clarkii</i>	Podicipedidae	IBR	2
Gadwall	<i>Anas strepera</i>	Anatidae	SCN	3
Greater scaup	<i>Aythya marila</i>	Anatidae	ALV, SUI	3
Hybrid duck	—	Anatidae	IBR	1
Mallard	<i>Anas platyrhynchos</i>	Anatidae	SCR, SCN	4
Pied-billed grebe	<i>Podilymbus podiceps</i>	Podicipedidae	IBR	1
Wood duck	<i>Aix sponsa</i>	Anatidae	IBR	2
Bufflehead	<i>Bucephala albeola</i>	Anatidae	SCN	1
Raptors				
Barn owl	<i>Tyto alba</i>	Tytonidae	SFO	3
Red-tailed hawk	<i>Buteo jamaicensis</i>	Accipitridae	SFO, OAK	5
White-tailed kite	<i>Elanus leucurus</i>	Accipitridae	SFO	2
Other				
American avocet	<i>Recurvirostra americana</i>	Recurvirostridae	OAK	3
Canada goose	<i>Branta canadensis</i>	Anatidae	IBR, SCR	2
California gull	<i>Larus californicus</i>	Laridae	SCN, OAK	1
Marbled godwit	<i>Limosa fedoa</i>	Scolopacidae	IBR	1

* OAK, Oakland International Airport; IBR, International Bird Rescue; SCN, Sulphur Creek Nature Center; SFO, San Francisco International Airport; ALV, Alviso Boat Dock; SUI, Suisun Bay; SCR, Sacramento International Airport.

RESULTS

Parasite survey

During the course of the study, 57 avian hosts of 21 different species were examined for intestinal helminths (see Table I). We sampled 14 birds from Oakland International Airport, 10 from San Francisco International Airport, 6 from Sacramento International Airport, 9 from Sulphur Creek Nature Center, 11 from International Bird Rescue, 2 from the Alviso Boat Dock, and 1 from Suisun Bay. These included 5 species from the family Ardeidae, 7 from Anatidae, 2 from Accipitridae, 2 from Podicipedidae, 1 from Laridae, 1 from Rallidae, 1 from Scolopacidae, and 1 from Tytonidae. Birds from airports were collected in the spring, birds from the rescue centers were collected through the summer, and the birds from the hunting stations were collected during winter. The most common bird families sampled were the Ardeidae, with 19 individual hosts, and the Anatidae, with 16 individual hosts.

Sixty-four helminth taxa were identified: 5 acanthocephalans, 24 nematodes, 8 cestodes, and 27 trematodes (summarized in Tables II–IV). The cestodes were the most abundant, with 19,766 total specimens found. The nematodes had the highest infection prevalence, with 75% of birds infected. Total parasite richness per host species ranged from 0 in the white-tailed kite to 16 in the gull. The abundance ranged from 0 to nearly 10,000 (9,900 specimens of the cestode *Diplophallus coli* were detected within an American avocet). Although no helminth species were shared among all host

species, the following parasites were detected: in 5 host species, *Posthodiplostomum* spp. and *Capillaria* spp.; in 4 host species, *Tetrameres* spp; in 3 host species, *Contracaecum* spp., *Polymorphus* spp., *Southwellina hispida*, *Ascocotyle* spp., *Echinoparyphium* spp., *Notocotylus* spp., and *Fimbriaria fasciolaris*; in 2 host species, *Desmidocerella numidica*, *Diplostomum spathaceum*, and *Microsomacanthus* spp. The remaining species or genera infected only 1 host species. Due to the freezing process, many of the helminths were difficult to identify to species, especially the cestodes where hook number and arrangement are often crucial and vulnerable to loss due to freezing. There were 13 unidentifiable infections involving cestodes, 1 unidentifiable acanthocephalan, and 6 unidentifiable nematode infections. The remaining parasites were identified to order, family, genera, or species (see Tables II–IV).

Bird life history trait analysis

The phylogenetic model performed best ($\text{elpd}_{100} = -92.5$, $\text{SE} = 3.8$), but the varying intercept model had comparable support ($\text{elpd}_{100} = -92.7$, $\text{SE} = 3.8$). The simplest model was not as well supported ($\text{elpd}_{100} = -93.8$, $\text{SE} = 4.6$), but overall these models performed similarly. Large clutch sizes and migration were associated with higher parasite richness (posterior probability [pp] = 0.94 and 0.99, respectively, from the phylogenetic model), and herbivory was associated with lower parasite family richness (pp = 0.98) (Fig. 2). Estimated coefficients were comparable across the three models, but the models with varying intercepts tended to produce estimates with wider intervals (Fig. 3). On

TABLE II. Prevalence (P, percentage of birds infected) and infection intensity (In, average number of parasites per infected host) of parasites of the Accipitriformes, Gruiformes, and Charadriiformes. Dashes indicate that no parasites of that species were recovered from that bird species.

Helminth taxon	American avocet (n = 3)		American coot (n = 1)		Barn owl (n = 3)		California gull (n = 3)		Marbled godwit (n = 1)		Red-tailed hawk (n = 5)		White-tailed kite (n = 5)	
	In	P	In	P	In	P	In	P	In	P	In	P	In	P
Acanthocephala														
<i>Profilicollis altmani</i>	—	—	—	—	—	—	44.0	33.3	—	—	—	—	—	—
<i>Southwellina hispida</i>	—	—	—	—	—	—	—	—	—	—	3.0	20.0	—	—
Nematoda														
<i>Capillaria recurvirostrae</i>	5.7	100.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cosmocephalus obvelatus</i>	—	—	—	—	—	—	22.0	33.3	—	—	—	—	—	—
<i>Echinuria heterobrachiata</i>	—	—	—	—	—	—	11.0	33.3	—	—	—	—	—	—
<i>Microtetrameres</i> sp.	—	—	—	—	—	—	—	—	—	—	5.0	20.0	—	—
<i>Paracuarua adunca</i>	—	—	—	—	—	—	11.0	33.3	—	—	—	—	—	—
<i>Skrjabinoelava kritscheri</i>	—	—	—	—	—	—	—	—	8.0	100.0	—	—	—	—
<i>Synhimantus laticeps</i>	—	—	—	—	7.5	66.7	—	—	—	—	—	—	—	—
<i>Viktorocara limosae</i>	—	—	—	—	—	—	—	—	2.0	100.0	—	—	—	—
Unidentified Nematoda	—	—	—	—	1.0	33.3	1.0	33.3	—	—	—	—	—	—
Cestoda														
<i>Aploparaksis</i> sp.	—	—	—	—	—	—	88.0	33.3	—	—	—	—	—	—
<i>Dendroterina herodiae</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Diplophallus coili</i>	3,968.0	100.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Nadejdolepis</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tetraphobius</i> sp.	—	—	—	—	—	—	13.0	33.3	—	—	—	—	—	—
<i>Wardium fryei</i>	—	—	—	—	—	—	324.0	33.3	—	—	—	—	—	—
Unknown Dilepididae	—	—	—	—	—	—	—	—	2.0	100.0	—	—	—	—
Unidentified Cestoda	—	—	—	—	1.0	33.3	—	—	—	—	—	—	—	—
Trematoda														
<i>Diplostomum spathaceum</i>	—	—	—	—	—	—	2.0	33.3	—	—	1.0	20.0	—	—
<i>Echinoparyphium</i> spp.	—	—	—	—	—	—	—	—	—	—	590.0	20.0	—	—
<i>Galactosomum humbargari</i>	—	—	—	—	—	—	4.0	66.7	—	—	—	—	—	—
<i>Himasthla alincia</i>	—	—	—	—	—	—	1.5	66.7	—	—	—	—	—	—
<i>Microphallus</i> sp.	—	—	—	—	—	—	145.0	33.3	—	—	—	—	—	—
<i>Neodiplostomum</i> sp.	—	—	—	—	—	—	—	—	—	—	2.0	20.0	—	—
<i>Notocotylus pacifier</i>	—	—	23.0	100.0	—	—	—	—	—	—	—	—	—	—
<i>Plagiorchis elegans</i>	—	—	—	—	—	—	—	—	3.0	100.0	—	—	—	—
<i>Posthodiplostomum</i> sp.	—	—	—	—	—	—	4.0	66.7	—	—	—	—	—	—
<i>Strigea elegans</i>	—	—	—	—	—	—	—	—	—	—	8.0	20.0	—	—
Unidentified Diplostomatidae	—	—	—	—	—	—	—	—	—	—	1.0	20.0	—	—
Unidentified Echinostomatidae	—	—	—	—	—	—	1.0	33.3	1.0	100.0	—	—	—	—
Unidentified Heterophyidae	—	—	—	—	—	—	39.5	66.7	—	—	—	—	—	—
Unidentified Schistosomatidae	—	—	—	—	—	—	1.0	33.3	—	—	—	—	—	—

average, migratory birds supported twice as many parasite families relative to nonmigratory birds, and carnivorous birds had 30% more parasite families than herbivorous birds.

DISCUSSION

Our results revealed a high diversity of parasites in bird hosts within the Bay Area relative to previous studies done within this region (Hoberg et al., 1989; Ching, 1990; Baker et al., 1996), with 64 taxa of intestinal helminths detected among the bird hosts examined. In total, we analyzed 57 birds, representing 21 species and 8 families, including raptors, egrets, herons, ducks, and other waterfowl. Variation in parasite richness within bird hosts was associated with life history traits, especially the migratory status

of the species, its clutch size, and dietary preferences, even after controlling for the phylogenetic relationships among host species.

Overall, we found high β diversity, such that there were no parasite taxa found in every bird species. The Trematoda had the highest diversity of parasites (27 taxa), likely because many of the examined host species spend significant time in aquatic systems (Rodewald, 2015), where many trematodes occur or are transmitted (Schmidt and Roberts, 2009). Similarly, Ching (1990) studied the Western willet and dunlin in northern California and reported a high diversity of parasites (9 taxa), with several genera in common with the current study, such as *Himasthla* sp., *Aploparaksis* sp., and *Nadejdolepis* sp. In a study of fecal samples from 6 raptor species housed in a rescue center in the Bay Area, Baker et al. (1996) also reported a high prevalence of trematodes, which aligns with the current study. In contrast,

TABLE III. Prevalence (P, percentage of birds infected) and infection intensity (In, average number of parasites per infected host) of parasites of the Pelecaniformes and Charadriiformes. Dashes indicate that no parasites of that species were recovered from that bird species.

Helminth taxon	Black crowned night heron (n = 4)		Clark's grebe (n = 2)		Great blue heron (n = 3)		Great egret (n = 4)		Green heron (n = 3)		Pied-billed grege (n = 1)		Snowy egret (n = 5)	
	In	P	In	P	In	P	In	P	In	P	In	P	In	P
Acanthocephala														
<i>Polymorphus brevis</i>	14.5	50.0	—	—	—	—	—	—	1.0	33.3	—	—	—	—
<i>Southwellina hispida</i>	15.0	25.0	—	—	10.0	33.3	—	—	—	—	—	—	—	—
Unidentified Acanthocephala	—	—	—	—	—	—	1.0	25.0	—	—	—	—	—	—
Nematoda														
<i>Contracaecum micropapillatum</i>	33.0	25.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Contracaecum</i> sp.	—	—	—	—	4.0	33.3	—	—	3.0	66.7	—	—	—	—
<i>Contracaecum microcephalum</i>	—	—	—	—	—	—	—	—	1.0	33.3	—	—	—	—
<i>Desmidocercella numidica</i>	—	—	—	—	2.0	33.3	2.0	25.0	—	—	—	—	—	—
<i>Desportesius invaginatus</i>	—	—	—	—	—	—	3.0	25.0	—	—	—	—	—	—
<i>Eustrongyloides ignotus</i>	—	—	—	—	—	—	3.0	25.0	—	—	—	—	—	—
<i>Strongyloides</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tetrameres</i> sp.	1.5	50.0	—	—	—	—	—	—	—	—	—	—	5.0	20.0
Unidentified Tetrameridae	—	—	—	—	—	—	2.0	25.0	—	—	—	—	11.0	40.0
Unidentified Spiruina	—	—	—	—	—	—	3.0	25.0	—	—	—	—	2.3	80.0
Unidentified Nematoda	1.0	25.0	—	—	—	—	2.0	25.0	3.0	66.7	—	—	—	—
Cestoda														
<i>Dendrouterina herodiae</i>	—	—	—	—	—	—	—	—	—	—	—	—	86.0	20.0
Unknown Dilepididae	1.0	25.0	—	—	—	—	—	—	—	—	—	—	—	—
Unknown Cyclophyllidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Cestoda	5.0	25.0	524.5	100.0	—	—	1.0	25.0	—	—	830.0	100.0	—	—
Trematoda														
<i>Apatemon gracilis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ascocotyle</i> sp.	3.0	25.0	—	—	125.5	66.7	—	—	—	—	—	—	21.0	20.0
<i>Ascocotyle felippei</i>	7.0	25.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Clinostomum</i> sp.	—	—	—	—	—	—	7.0	25.0	—	—	—	—	—	—
<i>Posthodiplostomum minimum</i>	—	—	—	—	21.0	33.3	—	—	—	—	—	—	—	—
<i>Posthodiplostomum</i> sp.	23.0	25.0	—	—	—	—	10.0	75.0	8.0	33.3	—	—	—	—
Unidentified Echinostomatidae	10.0	25.0	11.0	50.0	—	—	—	—	—	—	—	—	—	—
Unidentified Schistosomatidae	—	—	—	—	—	—	—	—	—	—	—	—	1.0	20.0
Unidentified Strigeidae	1.0	25.0	—	—	—	—	—	—	2.0	33.3	—	—	—	—

Hoberg et al. (1989) studied spotted owls from Oregon, for which they reported a lower overall infection prevalence (71% vs. 92% in the current study) and a parasite community dominated by nematodes (rather than by trematodes, as seen here). One parasite genus that is consistently identified in all listed studies above, including our own, is the nematode *Capillaria* spp., which is ubiquitous.

The observation of the *Ribeiroia* sp. from a mallard duck was noteworthy because this parasite has been frequently recorded in snail and amphibian hosts in the Bay Area (e.g., Johnson et al., 2013), but it has not been reported in a local avian host. Parasites in the genus *Ribeiroia* can cause severe pathology in the amphibian host, including increased mortality and the occurrence of limb deformities such as extra, missing, and misshapen limbs or digits that are hypothesized to increase transmission to definitive hosts such as birds (Johnson et al., 2002; Wilson et al., 2005; Johnson and Hartson, 2009). Although *Ribeiroia* has been recorded in at least 40 bird and 5 mammal definitive hosts, relatively little is known about the importance of particular species in driving the landscape-level distribution of infection (Johnson and McKenzie,

2009). The nearest reports are from Oregon in a California gull (Price, 1931) and 2 reports from double-crested cormorants in California (Dubois and Mahon, 1959; Johnson et al., 2004). The rarity of *Ribeiroia* in the current study could have several explanations. Many of the birds examined here are known to feed commonly in both marine and freshwater habitats, and we lack specific habitat data for each specimen that could offer insight into recent feeding activity. The timing of collection could further affect the probability of detecting *Ribeiroia*, given that many of the hosts included here were collected in the spring and early summer, which could be before they acquire the infection locally. Lastly, previous research from amphibians suggests that *Ribeiroia* is more common at mid- to higher latitudes within the United States, which could explain how uncommon *Ribeiroia* was in the current study (Johnson and McKenzie, 2009).

Our analysis of bird life history traits revealed associations between parasite family richness and host migratory status, diet, and clutch size. On average, migratory species had roughly 2 times as many parasite taxa as nonmigratory species, which was particularly pronounced among the trematodes. Previous re-

TABLE IV. Prevalance (P, percentage of birds infected) and infection intensity (In, average number of parasites per infected host) of parasites of the Anseriformes. Dashes indicate that no parasites of that species were recovered from that bird species.

Helminth taxon	Bufflehead (n = 1)		Canada goose (n = 3)		Gadwall (n = 3)		Greater scaup (n = 3)		Hybrid duck (n = 1)		Mallard (n = 4)		Wood duck (n = 1)	
	In	P	In	P	In	P	In	P	In	P	In	P	In	P
Acanthocephala														
<i>Corynosoma constrictum</i>	—	—	—	—	—	—	—	—	—	—	7.0	25.0	—	—
<i>Polymorphus</i> sp.	—	—	—	—	5.0	33.3	—	—	—	—	—	—	—	—
Nematoda														
<i>Capillaria</i> sp.	23.0	100.0	—	—	1.0	33.3	15.0	33.3	—	—	2.0	25.0	—	—
<i>Echinuria</i> sp.	—	—	—	—	—	—	—	—	—	—	1.0	50.0	—	—
<i>Epomidiostomum uncinatum</i>	—	—	—	—	3.0	33.3	—	—	—	—	7.0	50.0	—	—
<i>Epomidiostomum erami</i>	—	—	2.0	33.3	—	—	—	—	—	—	—	—	—	—
<i>Streptocara californiensis</i>	2.0	100.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tetrameres fissispina</i>	—	—	—	—	1.0	66.7	3.0	33.3	—	—	1.0	25.0	—	—
<i>Tetrameres spinosa</i>	—	—	—	—	—	—	15.0	33.3	—	—	—	—	—	—
<i>Trichostrongylus tenuis</i>	—	—	246.0	33.3	—	—	—	—	—	—	—	—	—	—
Unidentified Tetrameridae	—	—	—	—	—	—	—	—	—	—	6.0	25.0	—	—
Unidentified Nematoda	41.0	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Cestoda														
<i>Fimbriaria fasciolaris</i>	—	—	—	—	—	—	—	—	31.0	100.0	28.0	25.0	4.0	100.0
<i>Microsomacanthus</i> spp.	—	—	—	—	5.0	33.3	48.0	33.3	—	—	—	—	—	—
<i>Nadejdolepis</i> sp.	—	—	—	—	—	—	71.5	66.7	—	—	—	—	—	—
Unknown Cyclophyllidae	—	—	—	—	8.0	33.3	—	—	—	—	—	—	—	—
Unidentified Cestoda	—	—	17.0	33.3	448.5	66.7	5,353.0	33.3	10.0	100.0	3.0	25.0	5.0	100.0
Trematoda														
<i>Apatemon gracilis</i>	—	—	—	—	—	—	—	—	1.0	100.0	—	—	—	—
<i>Cotylurus hebraicus</i>	—	—	—	—	—	—	9.0	33.3	—	—	—	—	—	—
<i>Echinochasmus</i> sp.	—	—	—	—	—	—	3.0	33.3	—	—	—	—	—	—
<i>Echinoparyphium</i> spp.	14.0	100.0	—	—	—	—	—	—	444.0	100.0	18.0	25.0	—	—
<i>Echinostoma</i> sp.	—	—	—	—	—	—	227.0	33.3	—	—	—	—	—	—
<i>Echinostoma trivolvius</i>	—	—	—	—	—	—	—	—	11.0	100.0	—	—	—	—
<i>Maritrema</i> sp.	—	—	—	—	6.0	33.3	—	—	—	—	—	—	—	—
<i>Notocotylus</i> spp.	2.0	100.0	—	—	—	—	1.0	33.3	—	—	—	—	—	—
<i>Odhneria odhneri</i>	20.0	100.0	—	—	—	—	—	—	—	—	—	—	—	—
<i>Psilochasmus oxyura</i>	—	—	—	—	—	—	19.0	33.3	—	—	—	—	—	—
<i>Ribeiroia</i> sp.	—	—	—	—	—	—	—	—	—	—	4.0	25.0	—	—
<i>Typhlocoelum</i> sp.	—	—	—	—	—	—	—	—	5.0	100.0	—	—	—	—
<i>Zygocotyle lunata</i>	—	—	—	—	—	—	1.0	33.3	—	—	—	—	—	—
Unidentified Diplostomatidae	—	—	—	—	—	—	—	—	—	—	2.0	25.0	—	—
Unidentified Gymnophallidae	—	—	—	—	—	—	—	—	—	—	—	—	12.0	100.0
Unidentified Heterophyidae	32.0	100.0	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified Strigeidae	26.0	100.0	—	—	—	—	1.0	33.3	—	—	—	—	—	—

searchers have suggested a positive relationship between migration and parasite richness could stem from a weakening of the immune system during migration (Buehler et al., 2008), a greater aggregation of hosts (Krauss et al., 2010), or exposure to a wider range of habitats and parasite types. The alternative hypothesis (migratory escape) has been suggested to lower parasite richness in migratory birds due to the opportunities migration provides for avoiding or leaving infections behind (Loehle, 1995; Altizer et al., 2011). Our data support the former hypothesis in which migratory birds have higher parasite richness (migratory exposure), although we acknowledge that our results were confined to the helminth community found within the gastrointestinal tract of these birds.

Our results also supported an effect of host diet, in which more carnivorous birds tended to support a more diverse parasite community relative to species that were predominantly herbivorous. This effect likely stemmed from the increased exposure to trophically transmitted parasites, as evidenced by the observation that the increase was strongest for the trematodes. The effect of diet on the bird parasite community was also analyzed by Santoro et al. (2012), who concluded that birds with more diverse feeding habits (generalist feeders) have a richer parasite community, likely because they consumed more potential intermediate hosts. We also found that birds with larger clutch sizes tended to have higher parasite richness, which is consistent with hypothesized trade-offs between a host species' investments in reproduction versus

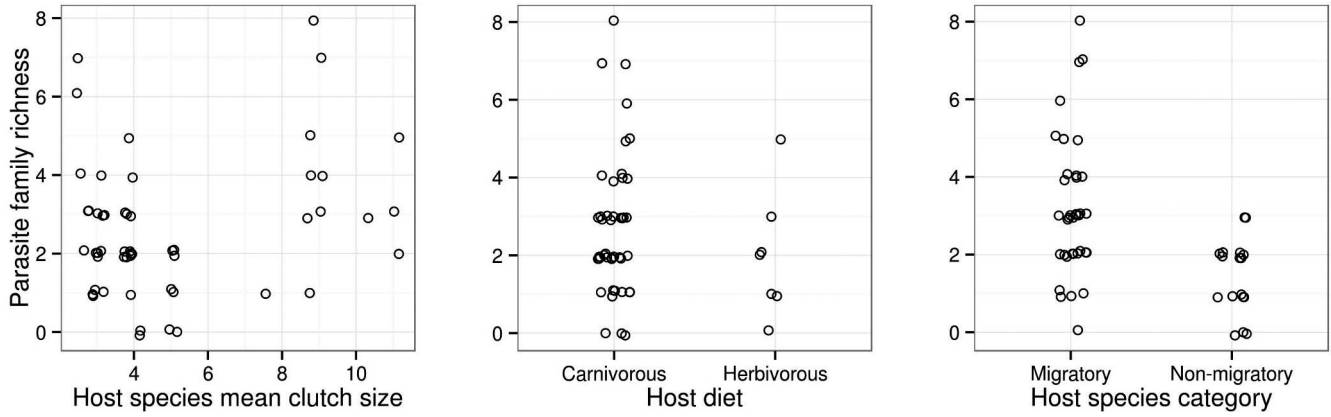


FIGURE 2. Raw data depicting relationships between parasite family richness and mean host clutch size, diet classification, and migration habit. Each point represents an individual bird, and the points have been jittered to reduce overplotting.

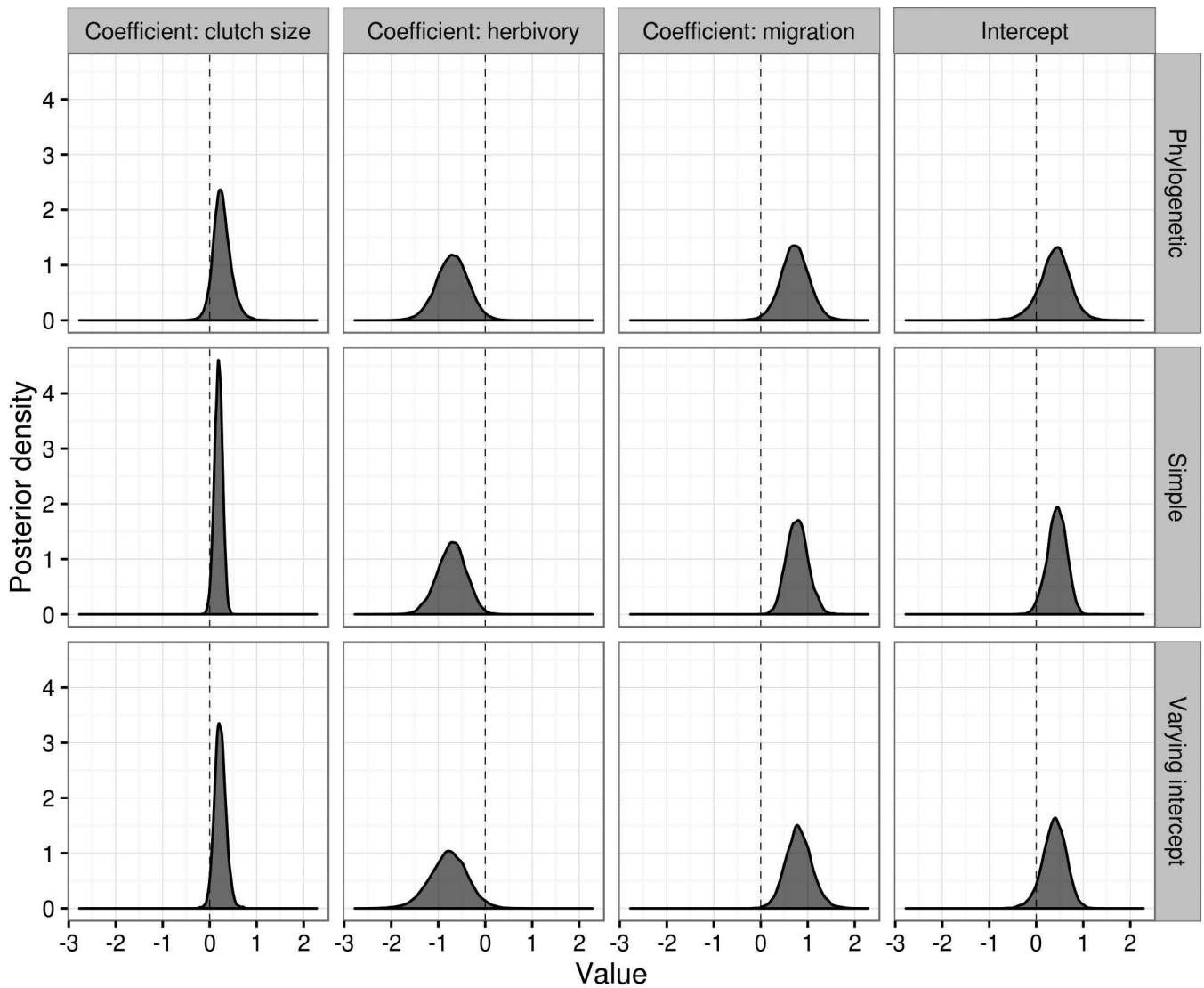


FIGURE 3. Posterior estimates for model coefficients. The y-axis represents the posterior probability density for each parameter, and each of our three models is represented as different columns.

immune defense (Ricklefs, 1992). There have been several studies that show a faster pace of life decreases the ability to fight infection (Lee et al., 2008; Johnson et al., 2012), and in birds has been hypothesized to be linked to less differentiation of immune cells and fewer antibodies (Ricklefs, 1992; Lee et al., 2008). Somewhat surprisingly, we found no association between host parasite richness and a species' longevity or body size, both of which have been suggested to increase parasite exposure in previous research (Cooper et al., 2012; Kamiya et al., 2014). Although body size has been well supported to have an effect on the parasite community in the host, other life history traits may have a stronger effect and thus mask the influence of body size when using a small sample size.

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