

Endohelminths from avian hosts in the San Francisco Bay Area of California, USA

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Abstract

Parasites can influence important ecosystem characteristics, such as biomass, biodiversity, food webs, and species interactions. Parasites of birds, in particular, offer a unique opportunity to test questions about parasites with complex life cycles (those that require more than one host for completion) and how host life history traits affect parasitic infections. For example, there is evidence that migratory versus non-migratory behavior in birds can affect the parasites present in 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 Bay Area of California to collect 57 raptors, waterfowl and herons for parasitological analysis. We performed detailed dissections of the gastro-intestinal tract and identified 64 taxa of parasites: 5 acanthocephala (thorny headed worms), 24 nematoda (roundworms), 8 cestoda (tapeworms), and 27 trematoda (flatworms). We then used generalized linear mixed modeling to determine how life history traits influenced parasite richness (number of taxa present) among bird hosts. We found associations with clutch size, diet and migratory status: parasite richness was greater in birds that were migratory, had larger clutch sizes and were carnivorous. The effect of both clutch size and diet is consistent with literature and has been linked to immune system function and parasite exposure respectively, whereas the effect of migration supports one of the two opposing hypotheses which are a topic of ongoing debate. These results add to the growing knowledge of how host life history can influence parasitic infections, especially with respect to the role of migration on parasite richness.

Introduction

There is a growing emphasis on the importance of parasites in the study of ecological communities and ecosystems. Historically, parasites have not been considered important because they are inconspicuous and collectively comprise only a small component of system biomass (Hudson *et al.* 2006). However, Kuris *et al.* (2008) showed that although a single individual may not contribute much to the biomass of a system, the combined parasite biomass within an estuarine marsh may be equal to that of a small herd of elephants. Not only has parasite biomass been underestimated, but also their biodiversity as experts estimate that between 30% and 50% of total biodiversity is composed of parasites (Poulin 2014). Correspondingly, growing evidence has illustrated the importance of parasites in food web structure (Dunne *et al.* 2013, Preston *et al.* 2014), interspecies interactions such as competition and predation (Hatcher *et al.* 2006), and in contributing to biodiversity patterns (Hudson *et al.* 2006). These recent advances in our knowledge of the role that parasites play demonstrate the significance of studying the parasites in a community.

Parasites of birds, in particular, offer a unique opportunity to ask questions about complex-life-cycle parasites. Parasites that have indirect or “complex” life cycles use a different host for each life stage to complete the life cycle and often use birds as the definitive host, in which parasites mature into their adult forms (Schmidt and Roberts 2009). Only in their adult form do the parasites become sexually mature (Schmidt and Roberts 2009). There are numerous examples of birds as the definitive host in all of the four major taxa of helminths. A helminth is a general term used to indicate one of four major taxa of macroparasites: the cestoda (tapeworms), the trematoda (flatworms), the nematoda (roundworms), and the acanthocephala (thorny-headed worms) (Schmidt and Roberts 2009). Using a bird as a definitive host is advantageous because

they have, on average, larger geographic ranges than mammals (Gaston 2003), and visit a high variety of habitats providing opportunities for transmission events between sites, thus driving distribution patterns for infection (Hartson *et al.* 2011).

How migration affects patterns of infection and parasite richness within birds is a topic of ongoing debate. A migratory bird might have more parasites than a non-migratory bird because they are exposed to more parasites during their journey. For example, Waldenstrom *et al.* (2002) argued that increases in blood parasites are a cost of migration for songbirds because the resident songbirds in Africa can act as a reservoir and immediately infect the migratory songbirds when they arrive. However, there is a competing theory called “migratory escape” in which migration reduces either the exposure to parasites or their persistence within hosts because sources of infection, such as feces, can be washed away before the next season (Loehle 1995). Heavily infected hosts may not leave for migration at the same time as healthy ones, thus causing a temporal separation between infective animals and non-infective animals (Hoye 2011). These two opposing theories are still currently in debate (Altizer *et al.* 2011; Bauer and Hoye 2014).

In addition to migratory behavior, there are many ways that life history traits can influence infection. Because organisms have a limited amount of resources to use for growth, reproduction, fighting infections and ensuring survival, there are tradeoffs between different life history traits. For instance, amphibians that reach maturity sooner and have shorter lifespans (faster pace of life) exhibited a higher parasite load and more pathology (physical symptoms caused by the parasite) following experimental infection than frogs with longer times to maturity and longer lifespans (Johnson *et al.* 2012). More specific to birds, Lee *et al.* (2008) analyzed 70 bird species and showed that antibody production is higher in slow-living species and birds with longer incubation periods. Furthermore, Ricklefs (1992) showed that birds that had a longer

incubation period had fewer hematozoan parasites and speculated that the mechanism behind this was more differentiation of immune cells during development. Body size is another trait that has been shown to affect the parasite community in a host; in a meta-analytic study of parasite richness and life history traits, Kamiya *et al.* (2014) found that body size was a well-supported and relatively strong positive predictor of parasite richness for all host types studied which included arthropods, gastropods, fishes, birds, mammals, fungi and plants. A larger body provides more niches and space to host parasites. In addition to the above mentioned traits, diet could also play a role to parasitic infections since many infections are transmitted through trophic interactions (consuming food). Santoro *et al.* (2012) studied the eating habits of 6 species of raptors and found that the more diverse the food items, the richer the parasite community. A bird with a more diverse eating habit would have greater exposure to different parasites.

Although the intestinal parasites of wading birds, raptors and waterfowl have been intensively researched in North America (MacDonald 1975; 1981; 1988), comparatively few studies have been conducted along the Pacific flyway, which includes the San Francisco Bay Area of California. The literature of waterfowl and raptor helminth surveys from this region consists of three studies that have little overlap with each other in terms of hosts examined, parasite species found, and patterns of infection. In 1989, fourteen spotted owls, *Strix occidentalis*, were collected from Western Oregon and analyzed for parasite composition (Hoberg *et al.* 1989). The authors identified 6 different species of parasites with an overall infection prevalence of 71% (percent of total birds with a parasitic infection). The species composition mostly consisted of nematodes while no trematodes were recovered. Ching (1990) analyzed the helminth communities in the Western willet, *Catoptrophorus semipalmatus inornatus*, and the dunlin, *Calidris alpina*, from the Bolinas Lagoon (Northern California). She

found 11 taxa of parasite from the Western willet and 17 in the dunlin. The species composition consisted mostly of trematodes, with only one species of nematode detected. The most recent study is of fecal samples from 18 raptor species residing in a rescue center in the San Francisco Bay Area which showed that 32% of birds were infected with a type of parasite (Baker *et al.* 1996). Of the helminths found, there was a high prevalence of unidentifiable trematode species, the nematode *Capillaria* sp. and ascarid nematodes.

Although poorly studied in bird hosts, many helminths in the Bay Area have been extensively researched by our own research laboratory from different hosts (Johnson *et al.* 2013b; Richgels *et al.* 2013), including amphibians, snails, insects, and fishes. Many helminths with interesting interactions exists in the Bay Area (Johnson *et al.* 2013a; Preston *et al.* 2014). To highlight the importance of understanding parasites in the bird hosts, *Ribeiroia ondatrae* is one of the dominant helminthes in the Bay Area with a complex life cycle. *Ribeiroia ondatrae* utilizes *Helisoma* snails as a first intermediate host, various amphibians as a second intermediate host, and birds or mammals for a definitive host (Johnson *et al.* 2004). *Ribeiroia ondatrae* has a severe effect on the amphibian host by causing malformations that include extra limbs, missing limbs, or grotesquely deformed limbs (Johnson *et al.* 2002). In the light of declining amphibian populations, parasites such as *R. ondatrae* are important to study because they are highly pathogenic to amphibians (Johnson *et al.* 2002). More information about definitive hosts in the Bay Area ecosystem is needed to complement previous work.

In the current study, we aim to fill in the knowledge gaps for the bird parasite community in the San Francisco Bay Area by assessing the helminth diversity of waterfowl, herons, egrets, ducks, and raptors. The specific objectives of the current study were to survey the helminth community in the Bay Area and create a database of parasites species present, explore the effect

of bird life history traits on parasite richness, and test the competing theories for how migration influences parasite richness. We expected to find a high overall diversity of parasites because birds typically host high parasite richness and there is evidence of a rich community in the Bay Area already. We also predict to find that body size, longevity, diet and clutch size influence the parasite community inside the host. In addition to the life history traits, we will examine the way migratory behavior affects the parasite richness in the host to see which of competing hypotheses our data support; whether migration causes parasite richness to increase or decrease.

Methods

Study system

Birds often host a wide diversity of parasites; among the most common parasites detected in birds are species of helminths (Schmidt and Roberts 2009). Numerous species of helminth utilize complex life cycles, which use multiple hosts for different life stages (Schmidt and Roberts 2009). For instance, the first intermediate host of a trematode typically involves a mollusk, which encounters an egg in the environment (Schmidt and Roberts 2009). Within the molluscan host, the parasite develops to a free-living stage emerges to locate a second intermediate host, which can be an amphibian, snail, fish, insect or a wide variety of hosts (Schmidt and Roberts 2009). The definitive host (typically bird or mammal) consumes the second intermediate host and the parasite develops into a sexually mature adult that produces eggs and spreads them back in the environment through feces (Schmidt and Roberts 2009). The life cycles of all four of the above taxa follow similar steps, although a wide variety of transmission mechanisms and hosts are used and there can be anywhere from one to four hosts in a lifecycle (Schmidt and Roberts 2009).

The San Francisco Bay Area of California is located on the Pacific flyway, which is one of four major routes that birds take for migration (*Migratory Bird Program* 2012). The Pacific flyway is the westernmost migratory route in North America and extends from Alaska into Mexico (Wilson 2010). The San Francisco Bay is the largest bay along the Western coast, and is where the Sacramento and San Joaquin rivers enter the Pacific Ocean (Conomos *et al.* 1985). The Bay Area offers a multitude of different kinds of wetlands that characterize the environment (Conomos *et al.* 1985). The Bay Area is one of the most important parts of the Pacific flyway as it serves as the breeding grounds, wintering grounds, or rest stops for many species of migratory birds; millions of birds visit or live in this area (Cormier and Pitkin 2008; Wilson 2010). This combination of wetlands and bird density provides perfect opportunities for parasite infection because transmission often occurs through the consumption of infected aquatic organisms (Schmidt and Roberts 2009). Our laboratory has sampled many of the aquatic organisms that might serve as prey for the birds in the Bay Area including tens of thousands of snails, thousands of amphibians, fish and insects. Here, we sought to complement and extend this work by examining birds as a host.

Specimen collection and species identification

To obtain samples of birds for helminthological survey, we collaborated with Oakland International Airport, San Francisco International Airport, Sacramento International Airport, Sulphur Creek Nature Center, International Bird Rescue, and two hunting locations in the National Wildlife Refuge system (Alviso Boat Dock and Suisun Bay). Airports often have depredation permits that allow them to cull any birds that are a danger to airplanes during takeoff which allowed for a great sampling opportunity. Bird rescue centers provided birds that were

unsuccessful rescues. At the hunting locations, a hunter removed the gastrointestinal tracts and froze them for later shipment.

After collections, birds were stored in a freezer (-20 C °) and subsequently thawed to remove their gastrointestinal tract. Gastrointestinal tracts were then shipped to the University of Colorado, Boulder, where they were stored at -20 C ° until dissection and parasitological examination. Dissection and identification techniques were similar to those described in Sepulveda and Kinsella (2011). The gastro-intestinal tract of each bird was examined for the four major taxa of helminthes by separating the esophagus, proventriculus, gizzard, stomach, duodenum, jejunum, and illium. In brief, each organ was examined separately, which started by washing the content of the gut into a petri dish for examination. The organ walls were then inspected for parasites still attached both on the inside and outside of the organ. The koilin 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 with a 200 µm mesh sieve followed by a 50 µm sieve, and thoroughly examined for any parasites using a stereo-dissection microscope at magnifications between 6.3 X and 63 X. Any species of helminths found were collected and preserved for later identification.

Detected parasites were preserved in an alcohol-formalin-acetic acid mixture (AFA), 70% ethanol, or 95% ethanol depending on future intended use. To facilitate morphological species identification, Semichon's Carmine or Mayer's Heamatoxylin were used to stain trematodes and cestodes followed by mounting in Canadian Balsam; nematodes were cleared in lactophenol and temporarily mounted. Available literature and dichotomous identification keys were used for identification: keys used for the nematoda included those by Yamaguti (1961) and Anderson *et al.* (2009), for the trematoda those Yamaguti (1958; 1971) Gibson *et al.* (2002;

2005; 2008), and Schell (1985), for acanthocephala those by Yamaguti (1963), and for the cestoda those by Yamaguti (1959), Schmidt (1986), and Khalil *et al.* (1994). Wherever possible, identification to the species level was achieved, but owing to poor specimen quality from the freezing process, many higher taxonomic level identifications were used. Specimens will be submitted to museums.

Statistical analysis of life history traits

To explore and identify factors contributing to observed differences among bird species in their parasite community composition and richness, we compiled a list of life history and demographic traits for each species using data published in literature (Table 2). Traits that were included in our analysis included maximum recorded longevity (years), migratory status (non-migratory vs. migratory), body mass (g), mean clutch size, diet preferences (herbivore vs. carnivore). Based on previous literature, we expected to find that longer lived host species would have few parasites (Cooper *et al.* 2012), migratory birds would host either a higher or lower parasite diversity (Waldenstrom *et al.* 2002), mean clutch size would be positively associated due to the allocation of resources into reproduction in the host species (Agnew *et al.* 2000), and that dietary habits would influence the parasite composition such that carnivores would host a higher diversity of parasites (Santoro *et al.* 2012). For the response variable, parasite family richness was chosen instead of parasite species richness because the taxonomic resolution at the species and genus level was inconsistent.

To analyze the influence of selected traits on parasite richness among birds, generalized linear mixed effects models (GLMM) were implemented with the statistical program R[®] and package “lme4.” The hybrid duck and Clark’s grebe were eliminated from this part of the study due to insufficient data in the life history traits. First, the collinearity of variables was tested

using a correlation matrix which shows the amount that any two variables correlate to each other. Two variables that are correlated can give disproportionately high significance to the statistical result and therefore must be addressed (Dormann *et al.* 2013). The maximum correlation coefficient allowed in the model was 0.70 (Dormann *et al.* 2013). For coefficients that approached this value, models were run with and without one of the predictors to see if the model fit changed. The distribution of parasite family richness was tested using Kolmogorov's goodness of fit test in JMP. Several generalized linear mixed models were fitted starting with all the predictor variables given in Table 2 and either bird host species or family as the random effects to account for bird individuals of the same species not being entirely independent from each other. The model was tested with and without random effects and simplest model was chosen. Terms of the model were eliminated one at a time from the full model until the lowest model AIC value was achieved. The lower the AIC value when comparing two models, the better the fit of the model (Burnham and Anderson 2004). Interactions were not tested because there were no biological bases for including an interaction. A p-value of less than 0.05 was used as a criterion for statistical significance in the data.

Results

Parasite survey

Between May 2012 and January 2013, 57 avian hosts of 21 different species were examined for intestinal helminthes (see Table 1). 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. There was a total of 5 bird species from the family Ardeidae, 7 species from Anatidae, 2 species 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 hosts and the Anatidae with 16 hosts.

A diverse group of helminths was found in the course of the study. Sixty-four helminth taxa were identified in the 21 species of birds: 5 acanthocephala, 24 nematoda, 8 cestoda, and 27 trematoda (summarized in Table 3). The trematodes were the most diverse with the highest species richness of 27. The cestodes were the most abundant with close to 20,000 total specimens found. The nematodes had the highest infection prevalence with 75% of birds infected with some species of nematode. The species richness found 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 coili* were detected within a single American Avocet). There were no helminth species that were shared among all 21 of the host species. Furthermore, there was large β -diversity, or large differentiation in the community composition between the host species analyzed. The following parasites were detected in 5 host species *Posthodiplostomum* spp., and *Capillaria* spp., in 4 host species *Tetrameres* spp, in 3 host species *Contraceacum* spp., *Polymorphus* spp., *Southwenellina hispida*, *Ascocotyle* spp., *Echinoparyphium* spp., *Notocotylus* spp., and *Fimbriaria fasciolaris*, in 2 host species *Desmidocercella numidica*, *Diplostomum spathaceum*, and *Microsomacanthus* spp., while the remaining species or genera only infected 1 host species. Due to the unavoidable freezing processes utilized for the collection of the specimens, many of the helminthes were difficult to identify to species, especially in the taxon cestoda where hook number and arrangement is often crucial and vulnerable to loss due to freezing. There were 13 unidentifiable infections involving

cestodes, one unidentifiable acanthocephalan, and 6 unidentifiable nematode infections. The remaining parasites were identified to order, family, genera, or species (see Table 3 for specifics).

Bird life history trait analysis

The distribution of parasite family richness closely aligned with the predicted values from a Poisson distribution, and we therefore used a Poisson response and log-link function in all models. With respect to the predictor variables, all of the correlation coefficients were <0.70 , suggesting collinearity among specific predictors was minimal; however, one variable exhibited a correlation close to this threshold (longevity and mass [$r=0.66$]). In our final models, we therefore explored iterations in which both variables in the pair were not included simultaneously to further minimize the effects of collinearity.

Based on generalized linear mixed effects models, bird life history strongly influenced patterns of parasite richness (see Table 4 for details). We found positive effects for migratory status and clutch size and negative effects of herbivory. For instance, migratory birds supported 2 times as many parasite families, on average, relative to non-migratory birds and non-herbivorous birds had 30% more parasite families than herbivorous birds. The models that included host species or host family as a random effect yielded similar fits. Host species was used as a random effect for all variations of the model to account for the lack of independence of bird individuals from the same species. The predictor variables that were dropped from the final model included body mass and longevity. The effects of migratory status were particularly strong, such that removal of this variable led to an increase in model AIC of 8 points (compared with delta AIC values of 2.4 and 3.0 when clutch size or herbivore were dropped, respectively).

Discussion

Our results revealed a high diversity of parasites in the Bay Area relative to other studies done within this region, with 64 taxa of intestinal helminths detected among the bird hosts examined. Overall, trematodes were the most diverse parasite group (27 different taxa), the cestodes were the most abundant (on average 374 per host), and the nematodes were most prevalent (75% of birds had a nematode infection). In total, we analyzed 57 birds representing 21 different species and 8 different families, including herons, ducks, raptors, and waterfowl. Through generalized linear mixed modelling, our analyses suggested that some of the variation in parasite richness within bird hosts was linked with important life history traits, especially the migratory status of the species, the clutch size, and its diet.

Based on the parasitological survey, several patterns of infection were identified. The acanthocephala had 18% prevalence (#birds infected/total birds) and 5 parasite taxa identified, the cestoda had 43% prevalence and 8 different taxa identified, the nematoda had 75% prevalence and 24 taxa identified, and the trematoda had 52% prevalence and 27 taxa identified. The trematoda had the highest diversity of parasites, most likely because many trematodes have aquatic lifestyles, meaning the intermediate hosts are aquatic animals, and many of the host species studied spend significant time in aquatic systems. The cestode diversity is most likely underrepresented in this study because parasites of the cestoda seem particularly vulnerable to degradation inside of the host which led to a reduced ability to identify to the species level. Overall, we found high β diversity, or the difference in parasite community between each host. There were no parasite species that were found in every bird species. This is in contrast to Santoro *et al.* (2012), who studied 6 species of raptors in Italy and reported that several parasitic species were present in all 6 host species. In our study, the most common parasite species

infected only 5 host species out of 21. This difference could be explained by the fact that the hosts in the Santoro *et al.* (2012) study were much more similar than the hosts in our study. Their study looked at predatory raptors from 2 different families, whereas the current study was expanded to 9 different families.

Our results have little overlap with previous studies, possibly due to the difference in host species examined, study locations and methods utilized. Hoberg *et al.* (1989) studied spotted owls from Oregon and their results differ from ours because not only did Hoberg *et al.* (1989) find the highest diversity in nematodes, but they didn't find any trematodes at all. There were no common species, but common parasite genera found were *Synhimantus* sp., *Capillaria* sp., and *Microtetrameres* sp.. Lastly, the percentage of hosts infected with a helminth parasite (# of infected birds/ total # of birds) in Hoberg *et al.* (1989) was 71% whereas we found 92% of birds were infected. The species differences in the parasite community and prevalence is most likely from a difference in the host species studied and different sampling environments. A more similar study design was done by Ching (1990) and their results matched slightly closer to ours. The study sites in Ching (1990) were in Northern California and were closer to ours, however the host species studied still differed as Ching studied the Western willet and dunlin. This similarity is reflected in the result that Ching (1990) found highest diversity in the trematoda. Additionally, there were several common genera, *Himasthla* sp., *Aploparaksis* sp., and *Nadejdolepisi* sp., although no identified species matched (Ching 1990). The most similar study was done by Baker *et al.* (1996) which showed similar trends in major taxa identified. This study is from the San Francisco Bay Area and shares the red-tailed hawk and barn owl as host species with our study. However, their study had different collection methods because they use fecal samples of captive birds. Baker *et al.* (1996) found a high prevalence of the trematoda which aligns with the current

study that the trematoda are diverse in the Bay Area. Of the nematoda, parasites of the genus *Capillaria* were reported, which may be common with the species of *Capillaria* found in the current study. One parasite genus that is consistently identified in all listed studies above including our own, is the nematode *Capillaria* spp.

One important parasite identified was of *Ribeiroia* sp. because parasites of this genus are prevalent in the Bay area in snails, fish and amphibians; however they have not been found in the definitive host. Searching for the definitive host is important because the definitive host can determine landscape level distributions. Being able to understand factors that affect infection patterns is important because *Ribeiroia* causes severe pathology in the amphibian host (Johnson *et al.* 2002). With amphibian populations on the decline, anything such as pathogenic parasites needs to be monitored so appropriate conservation efforts can be applied.

Beyond the parasitological survey, our analysis of bird life history traits revealed strong associations between parasite family richness and migratory status of the bird as well as weaker associations with the diet and mean clutch of the bird. The effect of diet on the bird parasite community was analyzed by Santoro *et al.* (2012) using non-metric multidimensional scaling (NMDS; an ordination technique); they concluded that birds with more diverse feeding habits have a richer parasite community. We also found an effect of diet, although the methods used and study design differed in the way we characterized the eating habits and statistical methods. Santoro *et al.* (2012) argued that the generalist feeders were exposed to more parasites than the specialist feeders because they were exposed to more potential intermediate hosts. Our study agrees with Santoro *et al.* (2012) because birds that are herbivorous are consuming fewer potential intermediate hosts since most intermediate hosts are types of animals. The diet of the bird directly affects how the bird becomes infected with parasites since most of the intestinal

parasites are trophically transmitted, whereas the clutch size of a bird can indirectly affect the parasite community in the host through tradeoffs with reproduction and immune system function (Ricklefs 1992). There have been several studies that show a faster pace of life decreases the ability to fight infection (Johnson *et al.* 2012; Lee *et al.* 2008) which in birds has been hypothesized to be linked to less differentiation of immune cells and fewer antibodies (Lee *et al.* 2008; Ricklefs 1992). Our study supports this hypothesis because the birds with larger clutch size (a trait that is characteristic of fast-paced birds) also had a higher parasite richness, possibly indicating a tradeoff between the ability to fight infection and reproductive efforts.

One of the most interesting findings was the strong, positive effect migration had on the parasite community within the hosts. There are two competing theories where migration may increase the distribution and transmission of parasites or it might decrease the transmission because the birds are experiencing different timings than when the host can be infected (Altizer *et al.* 2011; Bauer and Hoyer 2014). Some argue that the compromised immune system during migration (Buehler *et al.* 2008), a greater aggregation of hosts (Krauss *et al.* 2010) and other factors contribute to a positive relationship between migration and parasite richness. Others argue richness will decrease because the birds are temporally separated from infections by different timing of environmentally transmitted pathogens (Loehle 1995), that the lifecycles are disrupted by the inability to find appropriate intermediate hosts (Loehle 1995) and by the fact that infected hosts tend to depart later than uninfected hosts (Hoyer 2011). Our data support the former hypotheses that migratory birds have higher parasite richness. However, we had a limited view of each bird's infection status by only looking at the helminth community of the intestine. The mixed results imply that dynamics are more complicated and may differ based on traits of the disease such as the lifetime and modes of transmission.

Some overarching themes gathered from the current study are that a diverse parasite community exists in the birds of San Francisco Bay Area, and that life history traits can influence the parasite richness found. This study adds evidence to the ongoing debate about the effect migration has on parasite community in the host; specifically that migration may increase the richness found. In the future, an expanded study that gets a higher sample size of each species of bird would better characterize the parasite community as well as more strongly support the hypothesis about clutch size, diet and migration. To further untangle the way in which migration affects the parasite community here, a more targeted selection of host species could be utilized. Overall, the current study highlights some interesting aspects of the parasite community in bird hosts of the San Francisco Bay Area and shows the need for further investigation.

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Tables and Figures

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



	Scientific Name	Host Family	Host Code	Location(s)	N (total)
Hérons and Egrets					
Black crowned night heron	<i>Nycticorax nycticorax</i>	Ardeidae	BCNH	SFO,IBR	4
Great blue heron	<i>Ardea herodias</i>	Ardeidae	GBHE	SCR,OAK	3
Great egret	<i>Ardea alba</i>	Ardeidae	GREG	SCR,OAK	4
Green heron	<i>Butorides virescens</i>	Ardeidae	GRHE	IBR	3
Snowy egret	<i>Egretta thula</i>	Ardeidae	SNEG	SCN, OAK	5
Ducks, Grebes and Coots					
American coot	<i>Fulica americana</i>	Rallidae	AMCO	SCN	1
Clark's grebe	<i>Aechmophorus clarkii</i>	Podicipedidae	CLGR	IBR	2
Gadwall	<i>Anas strepera</i>	Anatidae	GADW	SCN	3
Greater scaup	<i>Aythya marila</i>	Anatidae	GRSC	ALV,SUI	3
Hybrid duck	-	Anatidae	HYDU	IBR	1
Mallard	<i>Anas platyrhynchos</i>	Anatidae	MALL	SCR,SCN	4
Pied-billed grebe	<i>Podilymbus podiceps</i>	Podicipedidae	PBGR	IBR	1
Wood duck	<i>Aix sponsa</i>	Anatidae	WODU	IBR	2
Bufflehead	<i>Bucephala albeola</i>	Anatidae	BUFF	SCN	1
Raptors					
Barn Owl	<i>Tyto alba</i>	Tytonidae	BANO	SFO	3
Red-tailed Hawk	<i>Buteo jamaicensis</i>	Accipitridae	RTHA	SFO, OAK	5
White-Tailed kite	<i>Elanus leucurus</i>	Accipitridae	WTKI	SFO	2
Other					
American avocet	<i>Recurvirostra americana</i>	Recurvirostridae	AMAV	OAK	3
Canada goose	<i>Branta canadensis</i>	Anatidae	CANG	IBR, SCR	2
Gull	<i>Larus sp.</i>	Laridae	LASP	SCN, OAK	1
Marbled godwit	<i>Limosa fedoa</i>	Scolopacidae	MAGO	IBR	1

Table 1. The list of bird hosts dissected during 2012–2013. Site acronyms are as follows: 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 – Sacramenton International Airport.

Host	Maximum Longevity	Migratory Status	Maximum Body Mass (g)	Mean Clutch	Diet Preferences
AMAV	Bird Banding Laboratory 2014	Demers <i>et al.</i> 2010	Ackerman <i>et al.</i> 2013	Ackerman <i>et al.</i> 2014	Ackerman <i>et al.</i> 2013
AMCO	Bird Banding Laboratory 2014	Alisauskas and Arnold 1994	Gullion 1952	Crawford 1980	Jones 1940
BANO	Bird Banding Laboratory 2014	Marti 1999	Colvin 1984	*Marti 1994, Otteni <i>et al.</i> 1972, Reese 1972, Mikkola 1983, Degroot 1983	Colvin and McLean 1986
BCNH	Bird Banding Laboratory 2014	Hothem <i>et al.</i> 2010	Gross 1923	Henny 1972	Henny <i>et al.</i> 2002
BUFF	Bird Banding Laboratory 2014	Gauthier 2014	Gauthier 2014	Erskine 1972	Gammonley and Heitmeyer 1990
CANG	Bird Banding Laboratory 2014	Jarvis and Cornely 1988	Chapman 1970	*Mowbray <i>et al.</i> 2002	Owen 1980
GADW	Bird Banding Laboratory 2014	Bellrose 1980	Bellrose 1980	Miller and Collins 1954	Gates 1957
GBHE	Bird Banding Laboratory 2014	Henny 1972	Bayer 1981	Pratt and Winkler 1985	Hom 1983
GREG	Bird Banding Laboratory 2014	Byrd 1978	Herring <i>et al.</i> 2008	Pratt 1974	Baynard 1912
GRHE	Bird Banding Laboratory 2014	Bent 1926	Niethammer and Kaiser 1983	Dickerman and Ganzalo Gavino 1969	Niethammer and Kaiser 1983
GRSC	Bird Banding Laboratory 2014	Kessel <i>et al.</i> 2002	Irving 1960	Fournier 2001	Kessel <i>et al.</i> 2002
LASP	Bird Banding Laboratory 2014	Winkler 1996	Jehl 1987	**Winkler 1996	Winkler 1996

MAGO	Bird Banding Laboratory 2014	Stiles and Skutch 1989	Gratto-Trevor 2000	Gratto-Trevor 2000	Recher 1966
MALL	Bird Banding Laboratory 2014	Bellrose and Crompton 1970	Krapu 1981	Dzubin and Gallop 1972	Swanson <i>et al.</i> 1985
PBGR	Bird Banding Laboratory 2014	Muller and Storer 1999	Muller and Storer 1999	Muller and Storer 1999	Wetmore 1924
RTHA	Bird Banding Laboratory 2014	San Fransisco Field Ornithologists 2003	Craighead and Craighead 1956	Preston and Beane 2009	Preston 1990
SNEG	Bird Banding Laboratory 2014	Ohlendorf <i>et al.</i> 1988	Palmer 1962	Jenni 1969	Hom 1983
WODU	Bird Banding Laboratory 2014	Hepp and Bellrose 2013	Hipes and Hepp 1995	Morse and Wight 1969	Swanson <i>et al.</i> 1974
WTKI	Bird Banding Laboratory 2014	Stendell 1972	Stendell 1972	Stendell 1972	Stendell 1972

Table 2. Host codes are given in Table 1. The body mass was the largest value available in literature, the clutch was average clutch size, the longevity was the obtained by using the longest living bird for that species. * The value was calculated as an average from different subspecies. **The clutch was calculated as a middle value of the range.

	AMAV (n=3)		AMCO (n=1)		BANO (n=3)		BCNH (n=4)		BUFF (n=1)		CANG (n=3)		CLGR (n=2)		GADW (n=3)		GBHE (n=3)		GREG (n=4)		GRHE (n=3)	
Helminth Taxon	In	P	In	P	In	P	In	P	In	P	In	P	In	P	In	P	In	P	In	P	In	P
Acanthocephala																						
<i>Corynosoma constrictum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polymorphus</i> sp.	-	-	-	-	-	-			-	-	-	-	-	-	5.0	33.3	-	-	-	-	-	-
<i>Polymorphus brevis</i>	-	-	-	-	-	-	14.5	50.0	-	-	-	-	-	-	-	-	-	-	-	-	1.0	33.3
<i>Profilicollis altmani</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Southwenellina hispida</i>	-	-	-	-	-	-	15.0	25.0	-	-	-	-	-	-	-	-	10.0	33.3	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	25.0	-	-
Acanthocephala																						
Nematoda																						
<i>Capillaria recurvirostrae</i>	5.7	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Capillaria</i> sp.	-	-	-	-	-	-	-	-	23.0	100.0	-	-	-	-	1.0	33.3	-	-	-	-	-	-
<i>Contracaecum</i> <i>multipaillatum</i>	-	-	-	-	-	-	33.0	25.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Contracaecum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.0	33.3	-	-	3.0	66.7
<i>Contracaecum</i> <i>microcephalum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	33.3
<i>Cosmocephalus</i> <i>obvelatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Desmidocercella</i> <i>numidica</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	33.3	2.0	25.0	-	-
<i>Desportesius invaginatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	25.0	-	-
<i>Echinuria</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinuria</i> <i>heterobrachiata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epomidiostomum</i> <i>uncinatum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	33.3	-	-	-	-	-	-
<i>Epomidiostomum crami</i>	-	-	-	-	-	-	-	-	-	-	2.0	33.3	-	-	-	-	-	-	-	-	-	-
<i>Eustrongylides ignotuus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	25.0	-	-
<i>Microtetrameres</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paracuaria adunca</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Skrjabinoclava kritscheri</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Streptocara</i> <i>californiensis</i>	-	-	-	-	-	-	-	-	2.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Strongyloides</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Synhimantus laticeps</i>	-	-	-	-	7.5	66.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tetrameres fissispina</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0	66.7	-	-	-	-	-	-
<i>Tetrameres spinosa</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tetrameres</i> sp.	-	-	-	-	-	-	1.5	50.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trichostrongylus tenuis</i>	-	-	-	-	-	-	-	-	-	-	246.0	33.3	-	-	-	-	-	-	-	-	-	-
<i>Viktorocara limosae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.0	25.0	-	-
Tetrameridae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.0	25.0	-	-
Unidentified Spiruida	-	-	-	-	1.0	33.3	1.0	25.0	41.0	100.0	-	-	-	-	-	-	-	-	2.0	25.0	3.0	66.7
Unidentified Nematoda	-	-	-	-	1.0	33.3	1.0	25.0	41.0	100.0	-	-	-	-	-	-	-	-	2.0	25.0	3.0	66.7
Cestoda																						
<i>Fimbriaria fasciolaris</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aploparaksis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dendrouterina herodiae</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplophallus coili</i>	3968.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Microsomacanthus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.0	33.3	-	-	-	-	-	-
<i>Nadejdolepis</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tetrabothrius</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Wardium fryei</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown Delepididae	-	-	-	-	-	-	1.0	25.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unknown	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.0	33.3	-	-	-	-	-	-
Cyclophyllidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.0	33.3	-	-	-	-	-	-
Unidentified Cestoda	-	-	-	-	1.0	33.3	5.0	25.0	-	-	17.0	33.3	524.5	100.0	448.5	66.7	-	-	1.0	25.0	-	-
Trematoda																						
<i>Apatemon gracilis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ascocotyle</i> sp.	-	-	-	-	-	-	3.0	25.0	-	-	-	-	-	-	-	125.5	66.7	-	-	-	-	-
<i>Ascocotyle felippeii</i>	-	-	-	-	-	-	7.0	25.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Clinostomum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.0	25.0	-	-	-
<i>Cotylurus hebraicus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplostomum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>spathaceum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinochasmus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinoparyphium</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinoparyphium</i> spp.	-	-	-	-	-	-	-	-	14.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinostoma</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Echinostoma trivolvus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Galactosomum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>humbargari</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Himasthla alincia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Maritrema</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6.0	33.3	-	-	-	-	-	-
<i>Microphallus</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Neodiplostomum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notocotylus pacifier</i>	-	-	23.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Notocotylus</i> sp.	-	-	-	-	-	-	-	-	2.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Odhneria odhneria</i>	-	-	-	-	-	-	-	-	20.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plagiorchis elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Posthodiplostomum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>minimum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21.0	33.3	-	-	-	-	-

<i>Posthodiplostomum</i> sp.	-	-	-	-	-	-	23.0	25.0	-	-	-	-	-	-	-	-	-	-	10.0	75.0	8.0	33.3
<i>Psilochasmus oxyura</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Strigea elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Typhlocoelum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Zygocotyle lunata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ribeiroia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diplostomatidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	10.0	25.0	-	-	-	-	11.0	50.0	-	-	-	-	-	-	-	-
Echinostomatidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gymnophallidae	-	-	-	-	-	-	-	-	32.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heterophyidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schistosomatidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified Strigeidae	-	-	-	-	-	-	1.0	25.0	26.0	100.0	-	-	-	-	-	-	-	-	-	-	2.0	33.3

Table 3 See following pages for Table 3 continued.

<i>Odhneria odhneria</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Plagiorchis elegans</i>	-	-	-	-	-	-	3.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
<i>Posthodiplostomum minimum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Posthodiplostomum</i> sp.	-	-	-	-	4.0	66.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Psilochasmus oxyura</i>	19.0	33.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Strigea elegans</i>	-	-	-	-	-	-	-	-	-	-	-	-	8.0	20.0	-	-	-	-	-	-
<i>Typhlocoelum</i> sp.	-	-	5.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Zygocotyle lunata</i>	1.0	33.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ribeiroia</i> sp.	-	-	-	-	-	-	-	-	4.0	25.0	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	2.0	25.0	-	-	1.0	20.0	-	-	-	-	-	-
Diplostomatidae	-	-	-	-	1.0	33.3	1.0	100.0	-	-	-	-	-	-	-	-	-	-	-	-
Echinostomatidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12.0	100.0	-	-
Gymnophallidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	39.5	66.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heterophyidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified	-	-	-	-	1.0	33.3	-	-	-	-	-	-	-	-	1.0	20.0	-	-	-	-
Schistosomatidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Unidentified Strigeidae	1.0	33.3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table 3 cont. Intensity (total # of individuals of parasite species Y in bird species X / # of infected birds of species X) and prevalence (# of birds of a species X infected with parasite Y / total # of birds of species X) of identified parasite taxa. Sample size = n. Bird species codes are given in Table 1.

	Estimate	Standard Error	z-value	p-value
Intercept	0.04734	0.26882	0.176	0.860
Migration (0 = non-migrant; 1 = migratory)	0.77906	0.2384	3.269	0.001*
Herbivore (0 = non-herbivore, 1 = herbivore)	-0.72156	0.33009	-2.186	0.029*
Mean clutch	0.07802	0.03613	2.159	0.031*

Table 4. The generalized linear mixed effects model p-values. The values are based off of non-scaled

data. The model was a better fit with host species as a random effect. *significant values

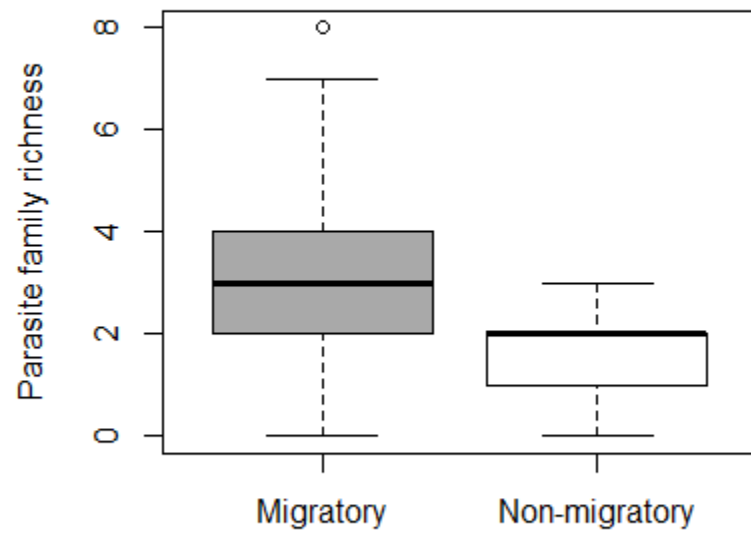


Figure 2. A box plot of parasite richness in migratory and non-migratory birds. On average, migratory birds had 2 times more parasites than non-migratory birds

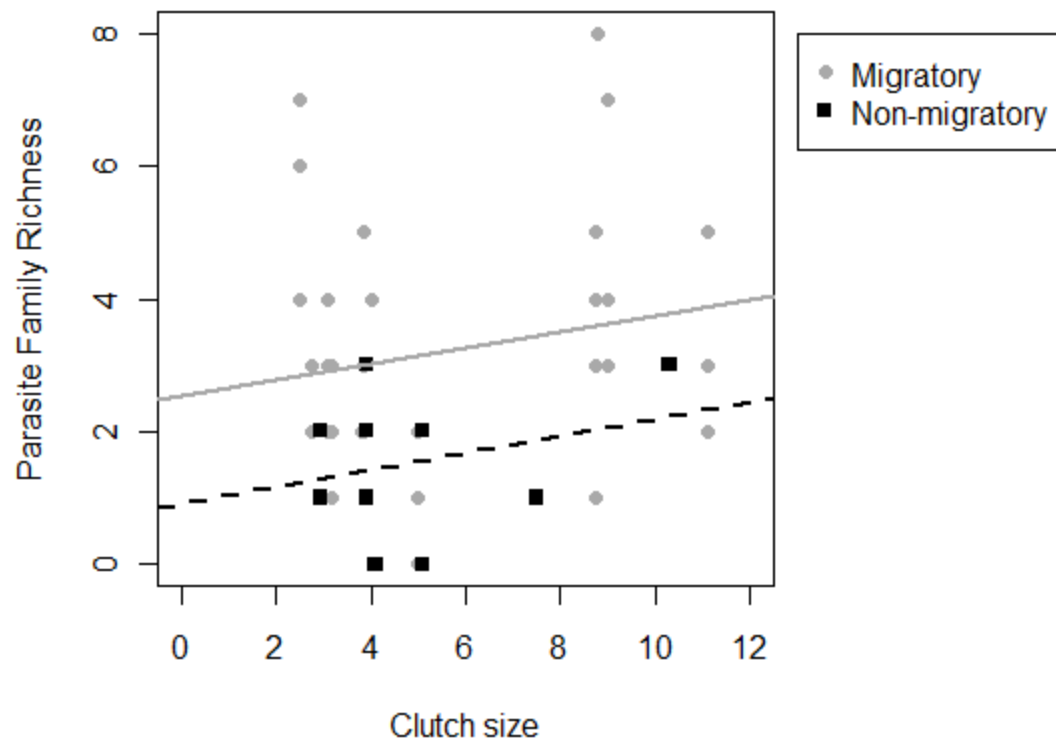


Figure 3. A bivariate scatterplot of parasite family richness as a function clutch size. Migratory birds are represented by the gray dots and line, whereas non-migratory birds are shown in black squares and dashed line. The lines of best fit were drawn using a simple linear model for the use of visual aid.

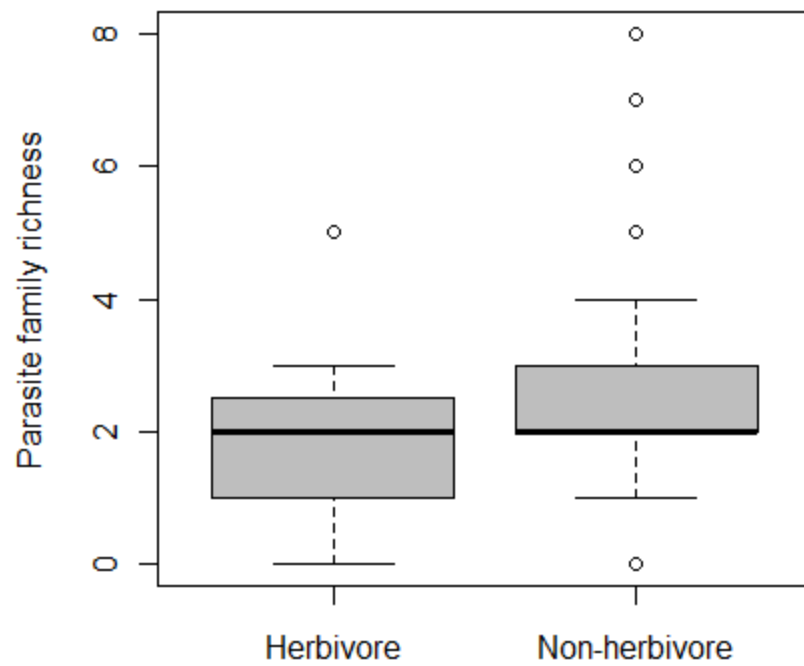


Figure 4. A box plot of the parasite richness in herbivorous and non-herbivorous birds. On average, the non-herbivorous birds had 30% higher parasite richness than herbivorous birds.