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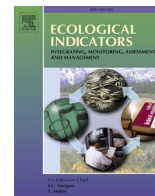
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## Original Articles

# Predicting consistent foraging ecologies of migrating waterbirds: Using stable isotope and parasite measurements as indicators of landscape use

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## ABSTRACT

The emergence of novel human pathogens is frequently linked with zoonotic events and human-wildlife interactions that promote disease transmission. Consequently, surveillance of wildlife populations for candidate diseases that could spread to humans is beneficial, but requires widespread collections of numerous samples. A legitimate means to acquire large sample sizes of waterfowl is through cooperation between researchers and hunters, who also work in concert with natural resource managers, landowners, and agricultural entities -e.g., aquaculture facilities. In addition to understanding the occurrence and spread of parasites and pathogens by birds, these samples can be used to answer questions about the ecology of various waterbird species. Body mass and morphometric data on hunter-donated specimen are useful for understanding bird condition and other dynamics of birds; however, when breast meat is removed prior to the acquisition of specimen weight, samples might not be as desirable. Here, we evaluate the utility of data obtained from a bird species that might be targeted by hunters and subsequently used to learn about their disease dynamics. Lesser Scaup (*Aythya affinis*) collected at aquaculture facilities were assessed for their stable isotope concentrations and parasites communities to learn about the birds' foraging ecology. Discriminant analyses designed to classify birds by the aquaculture pond type from which they were collected included isotope data, Principal Components derived from parasite community data of 7 types, and birds' body mass. We compared these to Double-crested Cormorants (*Nannopterum auritum*) feeding on catfish and found the two waterbird species exhibited different infracommunities of parasites. Furthermore, some scaup demonstrated fish aquaculture pond type fidelity. Bird body mass was an important metric to include in analytical models when all parasite datatypes were not available. However, the combination of stable isotope concentrations and parasite infracommunity data (that includes prevalence, abundance, volume, and energy use) in models resulted in host ecology differentiation equal or better than models where bird body mass was included. Hunter-derived samples should be encouraged as a means for sample acquisition and be considered as an approach for aquaculture-wildlife conflict management as the information that can be obtained through these samples is multifaceted.

## 1. Introduction

### 1.1. Aquaculture pond use can increase sample sizes needed for infectious agent surveillance

Emerging diseases in human populations are increasingly linked to wildlife interactions and crossover events where zoonoses are

transmitted from wild to domestic animals, people, and pets. As such, the One Health initiative was formed to link humans, animals, and the environment (Kelly et al., 2017; de Melo et al., 2020). To understand and defend against future disease outbreaks in human populations, surveillance of wildlife populations is paramount (Artois et al., 2009; Kuhn, 2020). Effective surveillance requires widespread testing programs that can evaluate the natural background levels and identities of endemic

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microbial pathogens (Ryser-Degiorgis, 2013; Kuker et al., 2018), ultimately leading to mediation strategies to prevent epidemics. While some strategies should focus on the treatment of humans post-exposure, such as vaccine and antibiotic development (Zinsstag et al., 2020), understanding wildlife dispersal behaviors and distribution can enhance predictions for transmission patterns. Identifying the underlying conditions that influence movements, interactions with congeners or other species, and overall resource exploitation provides fundamental understanding of potential exchanges that organisms and subsequent diseases might have with anthropogenic systems (Li et al., 2021).

Human-wildlife conflicts increase as urbanization modifies or causes the loss of natural habitats and natural systems are converted for agriculture (Lemly et al., 2000; Peterson et al., 2010) and urbanization (Larson et al., 2020). These transformations can modify or prohibit wildlife movement, limiting the ability of individuals or populations to disperse (Leidner and Haddad, 2011; Kimmig et al., 2020). Alternatively, aquaculture facilities provide semi- or permanently flooded conditions that attract a variety of avian species by which to forage (e.g., fish stocks) and loaf or rest (Hagy et al., 2014; Bai et al., 2018). The aquaculture industry has historically experienced conflict with waterbirds because they consume fish stocks, sometimes causing substantial economic losses (King, 2005; Dorr et al., 2012). Not all waterbirds consume farmed fish as some target invertebrate and vegetative components of aquaculture ponds (Clements et al., 2020a). Nonetheless, birds that forage and loaf on fish ponds can alter water quality through nutrient deposition via fecal matter (Rush et al., 2011) and introduce, spread, or facilitate the transmission of organisms (e.g., plants, invertebrates, fishes, parasites [Petrie et al., 2007; Reynolds et al., 2015]), which can also impact fish stocks (Overstreet and Curran, 2004). Further ecological complexity results as foraging birds can acquire parasites and pathogens from aquaculture facilities while interacting with these human-influenced food sources (Paladini et al., 2017). Ultimately, dispersing and migrating birds can transmit pathogens and parasites to natural communities through daily or seasonal movements (Dzikowski et al., 2003).

Fish farms attract a variety of waterbirds (Feaga et al., 2015; He et al., 2016) and are thus uniquely suited for providing abundant samples to help surveil bird populations for disease. Waterfowl hunters are attracted to fish farms given the abundance of scaup (*Aythya* spp.) and other species and subsequently provide collaborative opportunities with researchers by acquiring hunter-harvested waterfowl for laboratory inspection (Erwin, 2002; Schummer et al., 2020). This collaboration is favorable, as it helps to educate hunters on status of their harvested birds and increases sample sizes that ultimately improve disease surveillance programs.

Gaining a better understanding of how migratory waterbirds use aquaculture facilities is important because it can also elucidate their exploitation of other resources within landscapes, site fidelity, and how socio-biology (e.g., gregarious flocks) may influence transmission dynamics of infectious diseases (Kaminski and Elmberg, 2014; Casazza et al., 2021). As part of larger studies, we acquired data from experimentally collected birds to answer ecological questions for assessing landscape use of aquaculture facilities by foraging flocks of Double-crested Cormorants (*Nannopterum auritum*) and Lesser Scaup (*Aythya affinis*).

### 1.2. Migratory waterfowl as agents of dispersal

The Lesser Scaup is one of the most abundant waterfowl species in North America, but their estimated breeding populations have declined from an estimated 5.7 M to 3.6 M birds between 1970 and 2019, respectively (U.S. Fish and Wildlife Service, 2021). Reasons for the declines include anthropogenic stressors and landscape-scale environmental change (reviewed by Anteau and Afton, 2008). Parasites can also impact the physical condition of scaup, where blood parasite prevalence is negatively associated with feather production (wing length) and

percent body fat (Merrill et al., 2018). The digenean trematodes *Cyathocotyle bushiensis* and *Spaeriodiotrema* sp. cause hemorrhaging and development of cecal plaques (Hove and Scott, 1998) in the intestine of Lesser Scaup and negatively impact percent body fat (England et al., 2018). These parasites can be detrimental to scaup populations and are likely maintained in fish ponds, given the intermediate host populations that co-occur there. However, their impacts on fish stocks are not well demonstrated, likely because the aforementioned trematodes use invertebrates as intermediate hosts and do not infect fishes (Wisniewski, 1958; Quentin et al., 1986; Carreno, 2008), nor have they been shown to significantly impact fish yields (Lyndon, 2001).

Scaup consume invertebrates, like amphipods, but they will also opportunistically forage on small fishes (Clements et al., 2020b). Additionally, scaup using aquaculture ponds as stopover habitat during migration and winter can function as agents of dispersal for invasive plants and animals, notably the eggs of invasive fishes (Lovas-Kiss et al., 2020; Lin et al., 2021). This process occurs when live organisms or their propagules attach to skin or feathers or successfully resist digestion (Reynolds et al., 2015) and are transmitted between or among locations through defecation, potentially introducing detrimental species like cyprinid fishes into baitfish ponds (Lovas-Kiss et al., 2020). Thus, with frequent use of aquaculture ponds within a landscape, waterfowl landscape use could potentially homogenize food webs among natural food sources (e.g., rivers and lakes) and those within aquaculture ponds while ducks migrate and overwinter. Furthermore, if scaup preferentially select specific types of aquaculture over other foraging habitats, they could facilitate distinct community compositions within ponds that can be measured given identification of the proper endpoints.

The Double-crested Cormorant is a piscivorous pursuit-diving waterbird that has experienced substantial fluctuations in subpopulation sizes over the 20th century (Wires and Cuthbert, 2006). Cormorant populations have increased substantially through the late 1990s-early 2000s, with a 245% increase in breeding pairs in the U.S. Great Lakes from 1991 to 1997 (Tyson et al., 1999). The development of catfish aquaculture in the Mississippi Delta has also benefited populations of cormorants during winters (Glahn et al., 2000b). Contemporary cormorant populations are considered stable and growing and are lethally managed using practices which typically involve removing problematic birds, particularly amid aquaculture facilities (see Dorr et al., 2021 for a review).

Cormorants arguably conflict with aquaculture more frequently than scaup because piscivory by the former species directly depletes fish stocks (Glahn et al., 2000b). Moreover, cormorants can distribute parasitic helminths such as digenean trematodes *Austrodiplostomum* sp. (Locke et al., 2015; Rosser et al., 2016), *Hysteromorpha triloba* (Huggins, 1954; Lopez-Hernandez et al., 2019), and *Drepanocephalus auritus* (Griffin et al., 2014; Sheehan et al., 2016); and parasitic nematodes *Capillaria* sp. (Yabsley, 2008) and *Contracaecum* sp. (Margolis and Arthur, 1979; Dick et al., 1987). All of these parasites can affect growth and survival of farmed fishes. Although baitfish are vulnerable to cormorant predation, most conflicts between this species and the aquaculture industry occur on catfish facilities, where species like those that cormorants consume in natural environments occur in high densities (Glahn et al., 2000a). Thus, the predominance of homogenization of helminthic fauna in aquaculture ponds in areas of migration and winter use by cormorants will be mostly confined to catfish producers. Because cormorants do not have substantial overlapping feeding ecology with scaup, and are likely to use natural and farmed food sources differently, we consider the two bird species modeled here to exhibit independent behaviors despite co-occurring in the same broader landscape.

Baitfish aquaculture is common in the southeastern United States, where over 70 % of farmed baitfish are produced in the Mississippi floodplain (U.S. Department of Agriculture, 2019). Relative to the scaup objectives in our study, we focus on four types of baitfish aquaculture facilities: golden shiner (*Notemigonus crysoleucas*: GOSH), fathead

minnow (*Pimephales promelas*: BLFH), black crappie (*Pomoxis nigromaculatus*: BLCR), and sunfish (*Lepomis* spp.: NABG). Although some similarities exist among the facilities and ponds used in farming these species (U.S. Department of Agriculture, 2019), substantial variability exists among farms because they can vary in the degree and type of supplemental feeding (e.g., fish food) they receive, the types and frequencies of organisms (e.g., invertebrate prey, vertebrate predators, and parasites) with which they interact, and great attention to water management that includes maintenance of healthy water chemistry through oxygenation/circulation, drawdown, rotation of ponds (Meade, 2012; Stone et al., 2016). Moreover, different pond types can vary because of water depth, pond morphology, or fish densities (Clements et al., 2020a). While some facilities farm multiple species, the majority have specialized areas where ponds of the same type persist. These dynamics expose waterfowl to diverse food types and distinct foraging options that may influence patterns of differential use of aquaculture facilities based on their morphology, behavior (e.g., diving for food), and forage preferences (Clements et al., 2021). To illustrate, pond use by scaup during autumn–winter could range from feeding on natural or non-farmed food sources, to preference (i.e., specialist) for a single type of aquaculture. Alternatively, they might invoke a flexible (i.e., generalist) use of two or more farmed species (Fig. 1). Given some preference in forage type, we expect that differences in the use of aquaculture ponds by waterfowl can be identified.

### 1.3. Stable isotopes as indicators of landscape use and foraging ecology

If an organism exhibits specialist diet regimes because of differential landscape use, our ability to define its biogeochemical properties and host-parasite interactions increases. Moreover, we can use a combination of biogeochemistry (stable isotope ecology) and parasite community assessments (infracommunity ecology) to refine knowledge of foraging tendencies of wildlife. Stable isotope analysis (SIA) is useful for documenting food web dynamics and other important complex ecological relationships between organisms and their environments (Mantou et al., 2020; Careddu et al., 2021; Smith et al., 2021). Predictable differences in the ratio of heavier to lighter isotopes of various elements relative to an international standard (Newsome et al., 2007) occur through nutrient assimilation within organisms and their tissues, changes in nutrient sources among trophic constituents, and through hydrologic and geologic processes (Hobson, 1999; Katzenberg, 2008; Scholz et al., 2020). The practicality of SIA for defining feeding

behaviors is context-specific, as the trophic interactions of organisms can vary temporally and spatially, and when foraging behaviors are highly inconsistent, they will exhibit great variability in local abundances or distribution.

Here, we assign waterbirds to a feeding type relative to their biogeochemical signatures using SIA. Stable isotopes assessments have successfully been used to demonstrate foraging site fidelity in marine systems (Smith et al., 2021) and to estimate the degree of dietary specialization in terrestrial mammals (Scholz et al., 2020). Thus, we expected this technique to help us differentiate among birds that use their foraging landscape in different ways. Our two primary hypotheses were: 1) if birds consistently forage on the same prey base, ie, specialized landscape use, and do not move among different pond types when foraging, distinct SIA values should be detectable within the tissues of these birds; 2) alternatively, if there is no preference in pond type and movement of birds among ponds is frequent and random, the classification of bird collection location would be indistinguishable from a null model, or random assignment of pond type.

### 1.4. Parasites as indicators of foraging ecology

Parasites that are transmitted among hosts through consumptive interactions, or trophically-transmitted parasites, serve as biological indicators of connected links in food webs (Lafferty et al., 2008). As such, parasite communities can be used to recreate food webs. This process assumes that A) parasite presence and composition reflect the local food web; B) host-parasite life histories are understood well enough and traceable among species; or 3) are generalist in nature and can be excluded from infracommunity assessments (Lafferty and Kuris, 2009). Host-specificity of parasites can vary widely both taxonomically and among life stages (Marcogliese, 2003). By using a combination of parasite prevalence (presence/absence) and frequency (numeric abundance) data, we can differentiate among parasite communities even when they exhibit similar taxonomic compositions (Sheehan et al., 2016). Here, in addition to biogeochemical signatures, we use parasite community composition to further differentiate among foraging types of waterbirds.

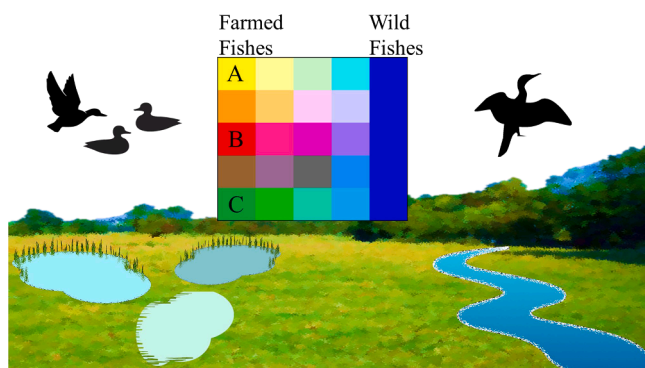
The combination of SIA and parasite community assessments to define host feeding ecology has been approached with limited success in previous assessments, where when used independently, they defined host ecology differently (Locke et al., 2012). Many previous works focused on host ecology using SIA and used individual parasite species or small components of the parasite infracommunity to further define host feeding trends. Some assessments included parasite taxa that were generalists (Sinisalo et al., 2006), violating assumption C (above) for the recreation of food webs. Here, we use all parasite species of the gastrointestinal tract to evaluate the entire infracommunity and remove generalist parasites that inhibit host differentiation. While we expected to detect differences in host feeding ecologies, if they existed, this technique has not previously been performed, so the degree of success, or whether the parasite and isotope data might contradict one another, leading to poor model performance was not anticipated.

The objectives of this assessment are threefold: 1) To learn whether Lesser Scaup exhibit consistent and specialized use of aquaculture ponds of different types; 2) to understand the degree to which trophic metrics (SIA and parasite infracommunities) can be used to differentiate landscape use; and 3) to determine if birds' body mass is a required variable in models or whether hunter-derived specimens can be used to assess SIA and parasites.

## 2. Methods

### 2.1. Model development

Hunter-collected birds that are donated for research are often 'breasted,' where the pectoral muscles are removed from the carcass and



**Fig. 1.** Lesser Scaup and Double-crested Cormorants interact with different components of the landscape in the Mississippi floodplain during the non-breeding season. Although both species use natural food sources and farmed species on aquaculture facilities, their diets do not overlap. Cormorants rarely visit baitfish ponds and were harvested from night roosts where they were likely to have been foraging on wild fishes (blue cells in center panel). Scaup, however, were harvested directly from baitfish ponds, of which they could have had substantial pond type fidelity (residing in cells “A,” “B,” or “C”) or a mixture of wild fish and or other pond types (any of the intermediate cells).

the remaining specimen remains intact. Although such samples are welcomed in research, as some information can be gained, body masses of 'breasted' birds cannot be obtained. Birds collected for this study were intact which allowed us to include (and exclude) body mass in a subset of the models that we developed. This helped us to learn the value of this metric in defining the feeding ecology of a bird.

Bird liver tissue samples were assessed for stable isotope concentrations with an Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS, Thermo Finnigan, San Jose, CA, USA) coupled with an elemental analyzer (Costech, Valencia, CA, USA). The ionized combustion product for all measured isotope values were mass-analyzed by differing mass/charge ratios (Craig, 1957; Giesemann et al., 1994). The analytical precision, based on the standard deviation of National Institute of Standards and Technology (NIST) (standard bovine liver [1577c]) and internal lab standard (tilapia [*Oreochromis* sp.]), for  $\delta^{15}\text{N}$  were  $\leq 0.23\text{‰}$  and  $0.06\text{‰}$ , respectively. Precision and accuracy values for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were  $\leq 0.15\text{‰}$  and  $-0.01\text{‰}$ , respectively, across all standards. Sulfur values were compared to five reference samples: NIST 1577c, internal standard tilapia muscle, USGS 42, NIST 8529, and NIST 8555. Precision for  $\delta^{34}\text{S}$  was measured at  $\leq 0.34\text{‰}$  with accuracy, based on USGS 42, at  $0.06\text{‰}$ .

Discriminant Analysis (DA) models are a multivariate tool that predicts the classification of objects based on empirical data for multiple variables that are used to build mathematical models. Model creation in a stepwise fashion (where one main effect is added incrementally in accordance with its statistical weight), helps to minimize misclassification, or the incorrect assignment of collected birds to a pond type. The variables of interest here are associated with the feeding ecology of scaup and cormorants: 1) bird sex, 2) host body size (mass), 3) differences in isotope ratios (carbon, nitrogen, sulfur), and 4) Principal Components (PCs, which are ordinations of the parasite community into combined variables) of the parasite infracommunity. Because waterbird sex and body mass can impact both biogeochemistry and parasite loads, we used parametric statistical analyses to test for patterns in variables and determine if they should be included in subsequent models. We performed Goodness of fit Chi-square tests to compare sex ratios among ponds and Analysis of Variance to compare body mass among ponds using two datasets: 1) One containing 'all birds' (scaup and cormorants) and 2) one restricted to only scaup data. Because we found no effect of sex on pond type use (Fig. S1), we excluded this variable from DAs, but we included the variable "weight" in half of the models, because we detected a difference in body mass among birds foraging on different types of ponds.

Lesser Scaup and Double-crested Cormorants can both host a high species richness of trophically-transmitted parasites (Hove and Scott, 1998; Sheehan et al., 2016; England et al., 2018), and we found parasite infracommunities comprised of species consistent with the literature. Some endoparasites were specific to cormorants, while others were specific to scaup, and one genus (*Tetrameres* sp. – excluded from models) infected both waterbirds given there is a small degree of dietary overlap between the two waterbird species. Parasite prevalence showed typical distributions for most species, where infection frequencies were relatively low and generated a dataset of predominately 0s that violated assumptions of normality and equal variance. Thus, a multivariate approach (Principal Components Analysis: PCA) was used to condense a series of species-rich datasets to two variables, or the first two components, for each one (McCune and Grace, 2002). We performed PCA on covariance matrices derived from parasites prevalence (presence/absence) data, count (intensity) data, parasite volume (the body volume of a given parasite multiplied by its intensity), and the energy flux (calories consumed per second by a parasite population), along with ranked data for count, volume, and flux (for descriptions of these, see Supplement) for each parasite species within every host bird. We retained the first two PCs for each PCA for inclusion in discriminant model development.

We designed four types of DA models in a stepwise fashion: 1)

**all\_birds\_weight**, where we included the data from all scaup and cormorants ( $n = 155$ ) – these models included bird body mass data, and each of the parasite PC options was included one (data type) at a time. We did this to determine which type of parasite PC data would be used in subsequent models (Table 1); 2) **all\_birds**, where the isotope data and the parasite PC axes for the most successful *all\_birds\_weight\_PC* model were included (Table 2), but body mass data were excluded; 3) **LESC\_weight**, where only data from Lesser Scaup ( $n = 72$ ) were used and bird mass was included as a main effect (Table 3); and 4) **LESC**, where only isotope and parasite data were included (Table 4) to classify Lesser Scaup to pond types. Chi-square Goodness of Fit tests compared the performance of each stepwise iteration of the models to detect any significant changes in classification success (Tables 1 & 2); however, we note that all models significantly outperformed the null of each model type.

## 2.2. Sample collection

We collected Lesser Scaup and Double-crested during the non-breeding seasons of 2016–2017 using 12-gauge shotguns. Scaup were collected from December through March (monthly collections of 7–11 birds, mean = 9, median = 9) on aquaculture ponds in eastern Arkansas and were observed foraging on the ponds. We processed 32 female and 39 male scaup. We collected cormorants from October through April (monthly collections of 3–8 birds, mean = 5.5, median = 6) during evenings, in known night roost sites in Mississippi and Arkansas (Clements et al., 2020b, Christie et al., 2021). The gastrointestinal tracts (GITs) of harvested birds received injections of ice-cold Phosphate Buffered Saline (PBS) immediately after collection to slow digestion (Clements et al., 2020b, Christie et al., 2021). Carcasses rested on ice until being moved to the Mississippi State Field Station necropsy lab for processing.

During necropsy,  $>0.1$  g samples of muscle, fat, liver, and blood were collected from each bird for stable isotope analyses, along with feathers and a claw as voucher samples. The upper GIT, consisting of the esophagus and stomach, was separated from the lower GIT, or the small intestine, caeca, colon, and cloaca. We split the lower GIT longitudinally to expose the lumen and soaked it in 150 ml of warm water to encourage parasites to release from the intestinal wall. Excess digestate was removed from the intestines by scraping, and the emptied tissue was placed in a bag and frozen for later visual confirmation of complete removal of parasites under stereomicroscope (Pritchard and Kruse, 1982). We fixed digestate in 150 ml of 20% neutral buffered formalin and performed an exchange with 70% ethanol after a minimum of 60 days. We searched the digestate for parasitic worms under stereomicroscope, counting all individuals encountered and preserving a subsample of each morphospecies in the taxon-appropriate fixative (Pritchard and Kruse, 1982). The upper GIT was emptied of dietary items and we removed, counted, and preserved any parasites within its lumen and under the internal lining of the ventriculus.

## 3. Results

We found 25 unique morphospecies of parasites among the 150 waterbirds examined (Fig. 2). Parasite species prevalence (presence/absence), numeric abundance (counts), infrapopulation volume, and infrapopulation energy flux, along with within-host ranked data for abundance, volume, and energy flux, were each condensed into 2 ordinal variables using PCA, resulting in 14 component variables. The parasite data type that minimized host misclassification was that for ranked abundance (Wt + N + S + C + PC1e and Wt + N + S + C + PC12e in Table 1) and used in subsequent models that tested for the importance of bird body mass in model performance (Tables 3 and 4). The full models that included all stable isotope and all parasite data type PCs were the top performers, reducing misclassification of scaup to pond type by 67 % and 55 % when host weight was included and excluded, respectively, when compared to the null. Thus, these models

**Table 1**

All birds\_weight model outputs created from both Lesser Scaup and Double-crested Cormorants (n = 155) with body mass data (Wt) included and constructed from stable isotope ratios (carbon [C], nitrogen [N], and sulfur[S]) and parasite infracommunities. Parasite community data were separated into 7 different types of data (a = prevalence, b = count, c = volume, d = energy flux, e = ranked count, f = ranked volume, g = ranked energy flux) for use in subsequent models that were then reduced to 2 variables using Principal Components Analysis. Models with parasite data included either the first PC (1x) or both PCs (12x). Model metrics include the number of individual birds (#) and the percent (%) misclassified, the model fit parameters based on the Entropy R-squared and the -2\*Log Likelihood of the Discriminant Analysis (DFA). Change (Delta) of iterative model performance for misclassifications were compared using a Chi-square Goodness of fit, where each stepwise progression was compared to the model containing one fewer variable.

Model	Misclassified		DFA		Delta		Goodness of Fit			
	#	%	R <sup>2</sup>	-2*Log	#	%	-2*Log	R <sup>2</sup>	X <sup>2</sup>	p
Null	93	80	/	/	/	/	/	/	/	/
<b>Full Model</b>	<b>28</b>	<b>18</b>	<b>0.60</b>	<b>147.4</b>	<b>-65</b>	<b>-70</b>	<b>29.7</b>	<b>0.14</b>	<b>59.4</b>	<b>&lt;0.001</b>
Wt	41	27	0.41	220.0	-52	-56	18.1	0.08	36.1	<0.001
PC1a	64	42	0.45	204.1	-29	-31	7.92	0.04	15.9	<0.001
Wt + PC1a	58	38	0.48	191.2	-35	-38	2.14	0.01	4.29	0.038
Wt + N	44	29	0.48	190.9	-3	-7.3	0.07	<0.1	0.15	0.703
Wt + N + S	45	29	0.54	171.0	+1	+2.2	0.01	<0.1	0.02	0.900
Wt + N + S + C	43	28	0.57	158.8	-2	-4.4	0.03	<0.1	0.06	0.801
Wt + N + S + C + PC1a	42	27	0.57	157.9	-1	-2.3	0.01	<0.1	0.02	0.899
Wt + N + S + C + PC12a	44	29	0.57	159.3	+2	+4.8	0.03	<0.1	0.06	0.800
Wt + N + S + C + PC1b	41	27	0.57	156.9	-2	-4.7	0.03	<0.1	0.07	0.799
Wt + N + S + C + PC12b	37	24	0.58	155.8	-4	-9.8	0.14	<0.1	0.27	0.601
Wt + N + S + C + PC1c	40	26	0.57	157.6	-3	-7.0	0.07	<0.1	0.15	0.701
Wt + N + S + C + PC12c	37	24	0.58	155.8	-3	-7.5	0.08	<0.1	0.16	0.694
Wt + N + S + C + PC1d	40	26	0.57	157.5	-3	-7.0	0.07	<0.1	0.15	0.701
Wt + N + S + C + PC12d	40	26	0.57	157.3	0	0	0.00	0.00	0.00	1.000
Wt + N + S + C + PC1e	<b>35</b>	<b>23</b>	<b>0.58</b>	<b>156.6</b>	<b>-8</b>	<b>-19</b>	<b>0.55</b>	<b>&lt;0.1</b>	<b>1.10</b>	<b>0.295</b>
Wt + N + S + C + PC12e	<b>33</b>	<b>22</b>	<b>0.57</b>	<b>156.8</b>	<b>-2</b>	<b>-5.7</b>	<b>0.04</b>	<b>&lt;0.1</b>	<b>0.08</b>	<b>0.780</b>
Wt + N + S + C + PC1f	42	27	0.57	159.8	-1	-2.3	0.01	<0.1	0.02	0.899
Wt + N + S + C + PC12f	40	26	0.57	158.8	-2	-5.0	0.03	<0.1	0.07	0.797
Wt + N + S + C + PC1g	43	28	0.57	158.2	0	0	0.00	0.00	0.00	1.000
Wt + N + S + C + PC12g	41	27	0.58	155.3	-2	-4.7	0.03	<0.1	0.07	0.799
Wt + N + S + C + PC1a + PC1e	45	29	0.56	160.8	+2	+9.8	15.2	0.07	30.5	<0.001

**Table 2**

All birds models built from stable isotope ratios (carbon [C], nitrogen [N], and sulfur [S]) and parasite prevalence including both Lesser Scaup and Double-crested Cormorants that was condensed, using the first two (1 alone and 1 and 2 together) principal components (PCs). Model metrics include the number (#) of individual birds and the percent (%) that were misclassified, the model fit parameters based on the Entropy R-squared and the -2 \*Log Likelihood of the Discriminant Analysis (DFA). Change (Delta) of iterative model performance for misclassifications were compared using a Chi-square Goodness of fit, where each stepwise progression was compared to the model with one fewer variable.

Model	Misclassified		DFA		Delta		Goodness of Fit			
	#	%	R <sup>2</sup>	-2*Log	#	%	-2*Log	R <sup>2</sup>	X <sup>2</sup>	p
Null	93	80	/	/	/	/	/	/	/	/
<b>Full Model</b>	<b>28</b>	<b>18</b>	<b>0.59</b>	<b>150.6</b>	<b>64</b>	<b>69</b>	<b>28.6</b>	<b>0.14</b>	<b>57.3</b>	<b>&lt;0.001</b>
N	61	40	0.27	270.1	-32	-34	6.61	0.03	13.2	0.003
N + S	51	33.3	0.41	218.4	-10	-16	0.70	< 0.1	1.40	0.238
N + S + C	45	29	0.44	205.5	-6	-12	0.27	< 0.1	0.54	0.462
N + S + C + PC1e	<b>37</b>	<b>24</b>	<b>0.45</b>	<b>202.4</b>	<b>-8</b>	<b>-18</b>	<b>0.53</b>	<b>&lt; 0.1</b>	<b>1.06</b>	<b>0.303</b>
N + S + C + PC12e	<b>35</b>	<b>23</b>	<b>0.45</b>	<b>201.4</b>	<b>-2</b>	<b>-5.4</b>	<b>0.04</b>	<b>&lt; 0.1</b>	<b>0.07</b>	<b>0.788</b>

**Table 3**

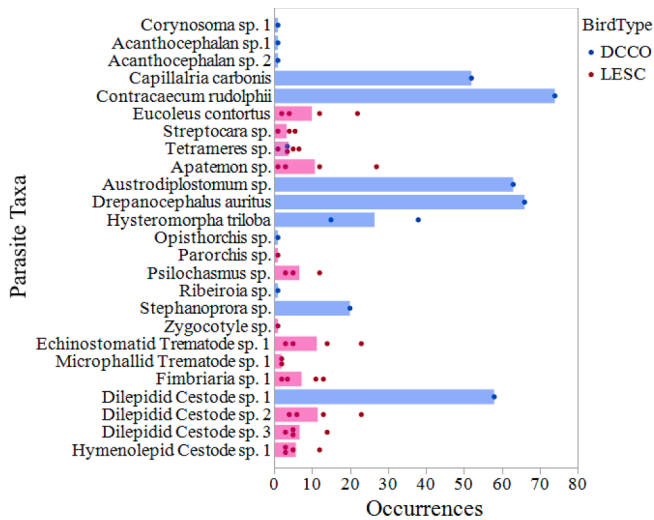
Models for classification of Lesser Scaup (LESC) that included weight (Wt) and were built from stable isotope values (carbon [C], nitrogen [N], and sulfur [S]) and parasite prevalence that were condensed, using the first two (1 alone and 1 and 2 together) principal components (PCs). Model metrics include the number of individual birds (#) and the percent (%) that were misclassified, the model fit parameters based on the Entropy R-squared and the -2 \*Log Likelihood of the Discriminant Analysis. Change (delta) of iterative model performance for misclassifications were compared using a Chi-square Goodness of fit, where each stepwise progression was compared to the model with one fewer variable.

Model	Misclassified		DFA		Delta		Goodness of Fit			
	#	%	R <sup>2</sup>	-2*Log	#	%	-2*Log	R <sup>2</sup>	X <sup>2</sup>	P2
Null	54	75	/	/	/	/	/	/	/	/
<b>Full Model</b>	<b>18</b>	<b>26</b>	<b>0.41</b>	<b>93.6</b>	<b>36</b>	<b>-67</b>	<b>19.1</b>	<b>0.19</b>	<b>38.7</b>	<b>&lt;0.001</b>
Wt	37	53	-0.12	176.3	-17	-31	4.49	0.05	8.97	0.027
Wt + N	38	54	-0.02	161.7	-1	+2.7	0.01	<0.1	0.03	0.867
Wt + N + S	33	47	0.08	147.7	-5	-13	0.35	<0.1	0.71	0.401
Wt + N + S + C	29	41	0.17	131.2	-4	-12	0.23	<0.1	0.46	0.498
Wt + N + S + C + PC1e	29	41	0.18	128.9	0	0	0.00	0.00	0.00	1.0
Wt + N + S + C + PC12e	29	41	0.19	128.4	0	0	0.00	0.00	0.00	1.0

**Table 4**

Models built for Lesser Scaup built from stable isotope values (carbon [C], nitrogen [N], and sulfur [S]) and parasite prevalence that was condensed, using the first two (1 alone and 1 and 2 together) principal components (PCs). Model metrics include the number of individual birds (#) and the percent (%) that were misclassified, the model fit parameters based on the Entropy R-squared and the  $-2 * \text{Log Likelihood}$  of the Discriminant Analysis (DFA). Change (Delta) of iterative model performance for misclassifications were compared using a Chi-square Goodness of fit, where each stepwise progression was compared to the model with one fewer variable.

Model	Misclassified		DFA		Delta		Goodness of Fit			
	#	%	R <sup>2</sup>	-2*Log	#	%	-2*Log	R <sup>2</sup>	X <sup>2</sup>	p
Null	54	75	/	/	/	/	/	/	/	/
<b>Full Model</b>	<b>24</b>	<b>34</b>	<b>0.30</b>	<b>110.6</b>	<b>-30</b>	<b>-55</b>	<b>13.2</b>	<b>0.14</b>	<b>26.5</b>	<b>&lt;0.001</b>
C	49	69	-0.10	177.0	-5	-9.2	0.44	0.01	0.89	0.347
C + S	40	57	-0.01	159.6	-9	-18	1.22	0.01	2.45	0.118
C + S + N	34	49	0.08	145.4	-6	-15	0.51	0.01	1.02	0.313
<b>C + S + N + PC1e</b>	<b>32</b>	<b>46</b>	<b>0.10</b>	<b>141.8</b>	<b>-2</b>	<b>-5.8</b>	<b>0.06</b>	<b>&lt;0.1</b>	<b>0.11</b>	<b>0.737</b>
<b>C + S + N + PC12e</b>	<b>32</b>	<b>45</b>	<b>0.11</b>	<b>140.8</b>	<b>0</b>	<b>0</b>	<b>0.00</b>	<b>0.00</b>	<b>0.00</b>	<b>1.000</b>



**Fig. 2.** Helminth parasites documented from the internal organs of Lesser Scaup (LESC: n = 83) and Double-crested cormorants (DCCO: n = 72) collected in Arkansas and Mississippi USA. While nearly all parasites were specific to their host species, some parasite species could have been shared as there is some overlap in diets of these birds.

demonstrate differentiation among scaup based on pond type and suggest some degree of individual consistency or preference for foraging habitats along birds' migration routes and wintering areas.

In all instances, the inclusion of stable isotope concentrations in predictive DAs lead to significant improvements in model performance compared to the null (Table 1). In contrast, when body mass data were included, the addition of stable isotope data did not substantively improve model performance, and in some cases, reduced classification accuracy. Parasite prevalence (presence/absence) and ranked abundance data enhanced model performance compared to the null ( $p < 0.001$ ), but when bird mass was included in these models, parasite data alone did not significantly enhance model performance. However, when stable isotope and parasite data were used together in models, the predictive performances of most DAs increased. The best prediction ability was achieved when we included all parasite data metrics. Thus, when desiring to understand habitat use of Lesser Scaup, we recommend using both stable isotope and parasite infracommunity information. Despite its important role in enhancing model performance, the models that did not contain bird body mass still significantly outperformed the null ( $p < 0.001$ ) and achieved 66 % classification accuracy.

Lesser Scaup demonstrated some degree of foraging specialization among the different types of ponds. Birds collected on GOSH ponds were frequently misclassified (97% of birds misclassified by at least one model) when compared to birds foraging on other pond types (63% misclassified by at least one model: Fig. 3).

#### 4. Discussion

We used two types of ecological data that reflect the diets of waterbirds: stable isotope concentrations and helminthic infracommunity composition. The integration of these data sources allowed us to evaluate their patterns of landscape use during the non-breeding season. Our predictive models differentiated among scaup collected on aquaculture ponds that contained different species of baitfish while using a feeding-guild distinct waterbird, the Double-crested Cormorant for comparison and to test for basic model performance. Our findings suggest that integrating data derived from stable isotopes and parasites can successfully predict the foraging ecology of a bird, given some consistent use of the landscape is manifested in the diet. Based on our results, some types of aquaculture facilities provide specific habitats of scaup, while other types of ponds appear to contain a more generalist diet. To our knowledge, this is the first assessment of its kind and could be a powerful tool in understanding the ecology of migratory birds as they traverse landscapes that are becoming increasingly impacted by human activities. Thus, we advocate that the origin and variation in sample availability, sample type, and sampling effort should be considered when designing waterbird studies. Moreover, the ecological utility of the sample itself will be context specific.

Differentiating how groups of birds use aquaculture ponds can be challenging because the base of the food web (the feeds, etc.), are similar among the different types of ponds and could be indistinguishable based on their biogeochemistry. Nonetheless, if birds exhibit strong enough pond type fidelity, could expect to find measurable differences in their parasite community assemblages. However, parasites can also become an ambiguous metric if the composition of the food webs are so similar that the same parasites occur in all pond types. Thus, models with poor classification performance could indicate landscape homogeneity in multiple ways. Despite this possibility, it appears that the combination of biogeochemistry and biological tags (parasites) can classify many Lesser Scaup to the correct pond type. We suggest that the misclassified birds could be individuals that simply do not show foraging/landscape type fidelity. Adding parasites, depending on the type of data being used to generate the covariance matrices that create the PCs, had a range of impact from minimal model decline (+3 or 1.9%) to moderate model improvement (Table 1). For this dataset, the largest improvement in model performance occurred when the total parasite volume of the population for each of the 8 most relevant parasites in the global (DCCO and LESCO combined) community was included, improving classification by 7.7%. This resulted in 79% correct classification for models that were derived from data for all birds and included body mass as a main effect.

Predictive models like DA help us learn about factors that define groups, and in turn, can be used to assign an object (e.g., foraging animal) to a specific group based on its characteristics (Sheehan et al., 2016; Shi et al., 2019). These approaches can also help us when asking questions pertaining to diet/habitat/landscape use specialization of individuals (variance), changes in group behavior/status, or the identity of unknown individuals (Quinn and Keough, 2002). In all instances, a



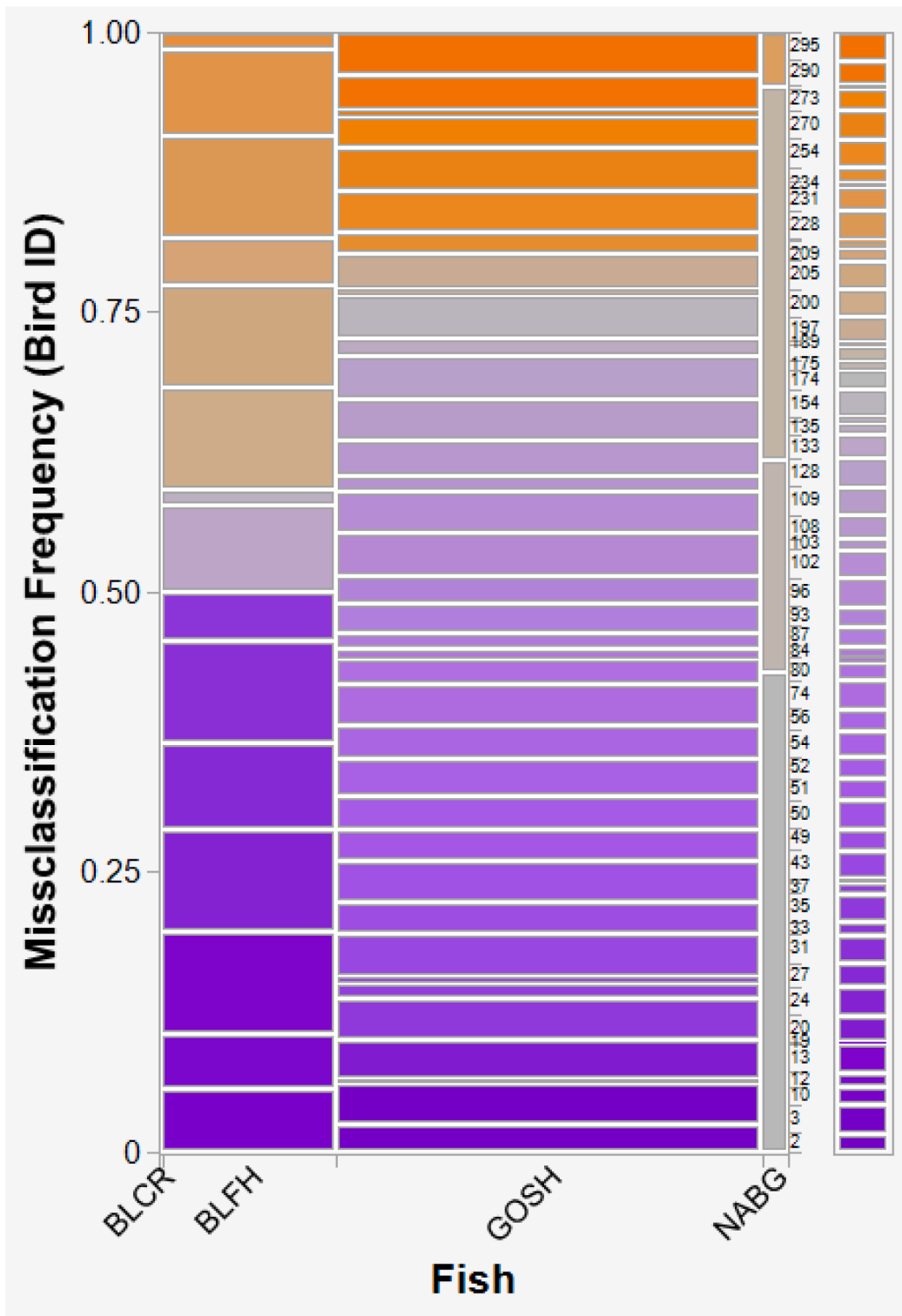


Fig. 3. Frequency of misclassification for Lesser Scaup by pond type. Black crappie: BLCR (1/7); Fathead minnow: BLFH (15/20); Golden shiner: GOSH (37/38); sunfish: NABG (4/6). In total, 57/71 Lesser Scaup were misclassified by one of the 14 models that included stable isotope and parasite community data.

reliable model should outperform the null where, for example, the frequency of correct assignments is tracked based on random sampling. Perhaps the more critical question is: By how much should a model outperform the null before we are willing to employ it? Because there is a plethora of applications for the models developed here, their measurements of success are context specific. We advocate that another important consideration is that the inclusion of additional parameters to

enhance model success will depend on the relative cost of data collection. For example, if adding information for a variable improves model classification success by 10 % but the collection of those data comes at a challenging temporal or financial cost, we might decide to leave the model as-is. Alternatively, if the cost of adding the data is relatively low and the benefit to model performance is substantial, collection of those data when designing assessments could be quite desirable.

In this study, when assessed independently, stable isotope concentrations successfully differentiated between the two bird species and correctly classified them 83/86 times (96%); there were three misclassifications of cormorants, suggesting the feeding ecologies of cormorants and scaup are dissimilar. However, use of the SIA without the parasite data integrated into the models, where host mass was available, was only partially informative. The combined use of parasite and stable isotope concentrations provided confirmational information on the feeding ecology of two waterbird species, while not producing redundant or duplicative results. Stable isotope concentrations will vary with local geology and hydrology, distance and connectivity to coastal systems, and along environmental nutrient gradients (Hobson and Wassenaar, 1999; Layman et al., 2007; Guiry, 2019). While informative, having additional information specific to food web interactions (i.e. the endoparasitic community) further differentiates among individuals, as parasitic infections indicate trophic interactions and established infections in a host (Lafferty et al., 2008).

Having both SIA and parasite data included in our models improved classification performance with and without the inclusion of host body mass. Models developed with bird body mass alone produced similar results to those for stable isotope concentrations (96% correct classifications; 3 misclassifications of DCCO); however, inclusion of parasite data improved model performances beyond that of body mass or stable isotopes alone. Data based on the prevalence (presence-absence) of the different species of parasites was sufficient to accurately split cormorants from scaup 100 % of the time (0 misclassifications of DCCO [ 83/83), confirming that the feeding ecologies of the two species is indeed different.

As expected, inclusion of parasite data can improve predictive model performance based on trophic groupings. We recommend, where feasible, that parasite data be considered as a metric that is regularly measured in ecological assessments of wildlife. Despite their utility, we realize there are challenges, and thus, some apprehension about including parasite infracommunity assessments in ecological studies of populations and communities. For example, collecting parasite data, while inexpensive in terms of equipment and supplies, can be time consuming post-collection. Moreover, to obtain the metrics used here, some degree of taxonomic expertise and the physical measurement (length, width, and height) for a subsample of each morphospecies identified is needed. Nonetheless, when included in predictive models, these data and other information derived from them (See Supplemental document), provide significant improvement in model performance. However, for each study, researchers should determine the merits of potential model improvements with levels of temporal, financial, or intellectual costs. Modern molecular techniques (eDNA and other metabarcoding techniques) exist to detect the presence of parasites more easily within hosts, but the presence of helminth DNA in the digestive tract of a waterbird does not confirm infection, only that it was consumed by the bird (Burreson, 2008). Admittedly, these techniques bear a greater financial cost than traditional parasitology methods that rely primarily on microscopy for helminth enumeration and identification (Binnicker and Kraft, 2015). Additionally, molecular techniques do not provide sufficient quantitative data that could be used to estimate infrapopulation volumes or energy flux. In our study, we found the inclusion of these metrics combined with count and prevalence data significantly improved model performance. The somewhat painstaking methods required to accumulate these data should be considered and methodological subsampling techniques can be deployed to enhance efficiencies while minimizing sampling errors.

As researchers seek to obtain large samples of wildlife for disease surveillance programs, hunter-donated specimens provide a meaningful source of sampling units that can also foster partnerships between hunters, aquaculture or other facilities, and the One Health community of practitioners. Animal carcasses used for swabbing and testing for known zoonotic and pathogenic agents that are endemic in bird populations can also be used to obtain information about their behavior and

ecology using SIA and parasite infracommunity assessments. When broader ecological questions are being addressed using hunter-donated birds and body mass data is not available because the pectoral muscles were removed, we find that both SIA and parasite infracommunity data should be considered for inclusion in assessments, as together they provide superior information on host ecology than merely either data type alone.

#### CRediT authorship contribution statement

**Kate L. Sheehan:** . **Brian S. Dorr:** . **Stephen A. Clements:** . **Terrel W. Christie:** . **Katie C. Hanson-Dorr:** Data curation, Methodology. **Scott A. Rush:** . **J. Brian Davis:** Conceptualization, Funding acquisition, Resources, Writing – review & editing.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.109038>.

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