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The influence of geographical location, host maturity and sex on intestinal helminth communities of the double-crested cormorant *Phalacrocorax auritus* from the eastern United States

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Abstract

Here the intestinal helminth infracommunities of 218 double-crested cormorants (*Phalacrocorax auritus*) from 11 locations in Alabama, Minnesota, Mississippi and Vermont are documented. Trematode infections were present in 98% of hosts; 65% of cormorants carried cestode infections, 4% were infected with acanthocephalans and 66% had nematode intestinal parasites. Parasite infracommunities of hosts collected on wintering grounds had higher richness and diversity than did birds collected on breeding grounds. Differences in parasite richness and diversity between male and female *P. auritus* were also detected, but not between immature and mature bird hosts. Parasite intensity did not differ by sex, maturity, or between breeding and wintering season. The most common parasite was *Drepanocephalus auritus* (*spathans*), which is recognized as a disease agent that negatively impacts the catfish aquaculture industry in the US. *Echinochasmus* sp. in double-crested cormorants is documented for the first time in the United States. We suggest that the differences observed among parasite infracommunities could be associated with the foraging distances travelled by *P. auritus* during breeding and wintering seasons, which is limited by allocation of parental care during the breeding season.

Introduction

The double-crested cormorant (*Phalacrocorax auritus*) is a large-bodied piscivorous waterbird ubiquitous in North America. In the population east of the Rocky Mountains, *P. auritus* breeds in the interior and Atlantic coasts of the United States and Canada. Eastern populations of *P. auritus* winter along the Gulf of Mexico and southern Atlantic coast to the Caribbean (Wires & Cuthbert, 2006; Dorr *et al.*, 2014a). These opportunistic pursuit-diving birds forage on the most abundant fishes between 2 and 25 cm in length (Campo *et al.*, 1993; Kirsch, 1995; Fenech *et al.*, 2004). In natural systems, the most abundant fishes can vary seasonally (Gido & Matthews, 2000; Anderson *et al.*, 2004; Coleman &

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Richmond, 2007; Dorr *et al.*, 2014b) and fish assemblages and their parasites can vary among water bodies. Consequently, cormorants eat an assortment of fishes and parasites as they move from one foraging ground to another. Thus, the diversity of a host's infracommunity offers an integrative estimate of the habitats that a bird has encountered (Sheehan *et al.*, 2016). Cormorants can be problematic to stocked ponds and aquaculture facilities, where predatory birds consume cultivated fishes (Jackson & Jackson, 1995; Overstreet & Curran, 2004; Dorr *et al.*, 2012; King *et al.*, 2012). Of particular concern in aquaculture is the echinostomatid trematode *Drepanocephalus auritus* (Kudlai *et al.*, 2015: previously reported as *D. spathans*), which infects *P. auritus* and causes mortality in juvenile farmed catfish that serve as intermediate hosts (Griffin *et al.*, 2014). During the breeding season, adult cormorants split their time between foraging and nesting activities.

Parental care of young is shared between the sexes in *P. auritus* (Anderson *et al.*, 2004) and, because birds must remain close to their nests during the breeding season, cormorants can be restricted to a relatively small foraging radius (e.g. 2.9–14.1 km; Custer & Bunck, 1992; Coleman *et al.*, 2005; Dorr *et al.*, 2012). A small foraging area can limit the variety of habitats and food types encountered and, thus, can limit the diversity of parasites acquired while foraging. On the other hand, in winter, the foraging range of *P. auritus* has been reported to exceed 300 km (King, 1996), suggesting that the variety of food items (and parasites) available to wintering birds could be greater. We note, however, that birds foraging around aquaculture facilities have smaller home ranges in winter compared to birds not affiliated with aquaculture (Dorr *et al.*, 2012).

The aim of this study was to determine whether parasite community dynamics reflect differences in host demography and seasonal behaviour. Infracommunity diversity within hosts can be used to indicate the richness of prey types that a host has encountered (Bush *et al.*, 1993, 1997; Sures & Streit, 2001; Thieltges & Poulin, 2016), and we hypothesize that birds collected during the breeding season, when their foraging radius is restricted, will have a lower diversity of intestinal helminths compared to birds collected during the winter non-breeding season. A subset of our collections include non-breeding immature birds (no nest guarding or brood provisioning), and we expect to find higher diversities of parasites in these birds during the breeding season compared to mature breeding adults. Because parental care is shared between male and female *P. auritus*, we expect similar infracommunities during the breeding season, and lower richness and diversity in wintering males, which forage more frequently in aquaculture facilities than females (Craig *et al.*, 2016).

Materials and methods

Collection and examination of cormorants

The US Department of Agriculture, Animal Plant Health Inspection Service, Wildlife Services (USDA/APHIS/WS) of Minnesota; the USDA/APHIS/WS National Wildlife Research Center; and the Band of Ojibwe, Division of Resource Management shipped the intestines or entire carcasses of *P. auritus* to Clemson University. Collections originated from 11 distinct geographic sites (see tables 1 and 2 for site descriptions and location). Bird carcasses or digestive tracts were frozen immediately after harvest and, in some cases, 70% ethanol was poured down the oesophagus to preserve stomach and intestinal contents prior to freezing (Reeder, 1951).

Intestines were processed in wildlife laboratories at Clemson University. Gastrointestinal tracts were defatted (solid fat bodies removed from exterior of intestine) prior to emptying of the contents by stripping the lining of the intestine by hand (manual scraping of the lining and mucosa: Rae, 2003). The intestinal lumen and contents were then washed with water in a 64-μm sieve, and fixed in 10% buffered formalin for morphological assessment. Contents were viewed under 3–70 × magnification (AmScope model ZM6745TN; AmScope, Irvine, California, USA) and all parasites were removed for identification and enumeration. Parasites were stored in 80% ethanol prior to identification (Yamaguti, 1958; Skriabin, 1964; McDonald, 1988; Gibson *et al.*, 2002, 2005, 2008; Forrester & Spalding, 2003) and a representative sample (up to five parasites) of most species from each locality was stained with acetocarmine, mounted in Canada balsam (Gower, 1939) and deposited at the US National Parasite Collection (accession numbers 108209–108247), Smithsonian National Museum of Natural History Department of Invertebrate Zoology, Washington, DC.

Data analysis

Measures of parasite diversity can be highly sensitive to rare species (e.g. species richness; Hanski, 1982) or reflect the evenness of abundance among the species present in an infracommunity (e.g. Shannon–Weiner entropy: Whittaker, 1972). Observed species richness within a host (S) is a relatively simple measure. Diversity indices [e.g. exponential Shannon entropy (exp(Shannon))] estimate richness while accounting for evenness, but require abundance data for their calculation (Whittaker, 1972; Spellerberg & Fedor, 2003). We chose to use exp-(Shannon) because once in the exponent form, Shannon–Weiner entropy provides a diversity estimate comparable to S, but declines based on the degree of dominant species present in an infracommunity (Jost, 2006). Thus, the difference between S and exp(Shannon) can be used to estimate the frequency of dominant vs. rare species (Leinster & Cobbold, 2012).

We calculated (S) and exp(Shannon) for the intestinal infracommunity of each host. Birds collected from the same locality at the same time comprise a sample group (see tables 1 and 2). Each sample group was categorized by season based on information provided from the source agency: the date of collection (breeding collections = May–August, table 1; winter collections = November–February, table 2), the approximate geographic location (latitude and longitude), sex and, when available, the reproductive age (immature vs. breeding adult).

Generalized mixed models are robust to non-normal data and are appropriate for tests where random effects must be accounted for (Bolker *et al.*, 2008). Values of S and exp(Shannon) were compared between reproductive age groups (immature and adult) of birds collected during

Table 1. Host collection information and mean parasite community estimates for *P. auritus* collected from their breeding grounds in Alabama (Lake Guntersville), Minnesota (Lakes Waconia, Leech and Wells) and Vermont (Lake Champlain).

Locality	Host collections					Parasite communities		
	Latitude	Longitude	Season	Year	Sample size	Abundance	Richness	Diversity
Lake Guntersville	34.3194	−86.316	Summer	2009	37	41 ± 5	10	3.2
Lake Waconia	44.861	−93.7846	Spring	2010	15	24 ± 6	7	2.9
			Spring	2011	15	74 ± 8	8	3.7
Leech Lake	47.1063	−94.372	Summer	2010	15	142 ± 32	8	3.7
			Spring	2010	14	75 ± 26	6	2.9
Wells Lake	44.2881	−93.3485	Spring	2010	15	44 ± 14	7	2.7
			Spring	2011	15	101 ± 22	9	3.8
Lake Champlain	44.5866	−73.38	Spring	2010	25	20 ± 3	8	2.4

the breeding season with a Generalized Linear Model (GZM with Poisson distribution – appropriate for count data estimated by S and exp(Shannon), and an over-dispersion correction: Gardner *et al.*, 1995) using JMP 12.1 Pro© (SAS Institute Inc., Cary, North Carolina, USA), and included sample group as a random variable. This tested whether there were significant infracommunity differences between breeding and non-breeding birds on the breeding grounds. After confirming no difference in parasite richness and diversity among age groups during the breeding season, we performed a second set of GZMs to test whether birds during the breeding season had higher parasite richness and diversity when compared to birds collected on the wintering grounds. A third set of GZMs tested for differences in parasite infracommunities between host sexes on breeding and wintering grounds. For this model, sample group was a random variable; first-order effects of sex and season and an interaction term for sex and season were used.

Results

The mean infracommunity intensity of the 218 *P. auritus* assessed was 63 worms. One bird had a singleton infection (one individual), and the highest intensity of infection was in a bird carrying 1488 parasites. The mean parasite richness was 3.7 species, with the highest richness found in birds from Bee Lake, Mississippi (MS); Lake Guntersville, Alabama (AL); and Wells Lake, Minnesota (MN) (tables 1 and 2). We observed 10 helminths from *P. auritus* (table 3) but identification to species was not possible for some. Thus, our results likely underestimate the species richness of intestinal parasites of *P. auritus*.

In all sample groups, the diversity estimate derived from exp(Shannon) was lower than the observed S, suggesting that dominant parasites were consistent among component communities (tables 1 and 2). As such, further reference to diversity encompasses both S and exp-(Shannon).

No differences in parasite infracommunity diversity were detected between mature (breeding birds) and immature (non-breeding) *P. auritus* at nesting sites where both age groups were present ($n = 72$: all localities in MN and Lake Guntersville, AL, table 3). The Generalized Linear Models comparing parasite abundance and diversity between breeding (collected on the breeding grounds; $n = 121$) and wintering birds (collected outside the breeding season; $n = 66$) revealed significant differences (table 4). Infracommunities of male *P. auritus* were consistently more diverse than females during the breeding season and in winter (parasite richness: $-$LogLikelihood $= 7.2$, $\chi^2 = 14.4$, $P < 0.01$; Shannon Diversity: $-$LogLikelihood $= 6.4$, $\chi^2 = 12.8$, $P < 0.01$; fig. 1), but infection intensities were similar between the sexes ($-$LogLikelihood $= 0.7$, $\chi^2 = 1.4$, $P = 0.70$).

Discussion

Many studies have documented the intestinal parasites of *P. auritus* at single locations or within a narrow region of its distribution, often focusing on a particular parasite taxon (Hutton, 1964; Threlfall, 1982; Flowers *et al.*, 2004; Dronen, 2009; Wagner *et al.*, 2012). This is the first study to document the intestinal parasite infracommunities of *P. auritus* collected from multiple localities within the eastern US. We report infections as previously observed in *P.*

Table 2. Host collection information and mean parasite community estimates in *P. auritus* collected from their wintering grounds in Alabama (Cat Island) and Mississippi (all other sites).

Locality	Host collections					Parasite communities		
	Latitude	Longitude	Season	Year	Sample size	Abundance	Richness	Diversity
Cat Island	30.3191	−88.21	Winter	2012	22	9 ± 1	7	2.7
Bee Lake	33.0476	−90.347	Fall	2010	5	61 ± 26	10	5.8
Mossy Lake	33.3474	−90.398	Fall	2010	11	48 ± 20	8	2.9
Port of Columbus	33.4798	−88.443	Winter	2011	10	75 ± 13	5	3.3
Swamp Roost	33.032	−91.08	Winter	2011	10	232 ± 142	7	4.3
Whittington Channel	32.9353	−90.543	Winter	2011	9	62 ± 21	8	3.9

Table 3. Mean prevalence and intensity of the ten parasite groups recovered from the intestines of *P. auritus*. Abbreviations for localities: Bee Lake (BL), Cat Island (CI), Lake Champlain (LC), Lake Guntersville (LG), Leech Lake (LL), Lake Waconia (LW), Mossy Lake (ML), Port of Columbus (PC), Swamp Roost (SR), Whittington Channel (WC) and Wells Lake (WL).

Parasite	Prevalence	Intensity	Localities
Trematoda			
Drepanocephalus auritus Kudlai, 2015	0.87 ± 0.02	38.2 ± 4.1	All sites
Hysteromorpha triloba Lutz, 1931	0.22 ± 0.03	1.6 ± 0.5	BL, LG, LL, LW, ML, PC, SR, WC, WL
Neodiplostomum sp.	0.19 ± 0.03	2.2 ± 0.8	BL, LG, LL, LW, ML, SR, WC, WL
Ribeiroia ondatrae Loos, 1907	0.01 ± 0.01	0.01 ± 0.01	LG, LW
Echinochasmus sp.	0.07 ± 0.02	1.2 ± 0.7	BL, CI, LC, LG, ML
Austrodiplostomum ostrowskiae Dronen, 2009	0.25 ± 0.03	8.6 ± 6.4	BL, CI, LC, LW, ML, PC, SR, WC, WL
Cestoda			
Dilepididae	0.65 ± 0.03	8.1 ± 1.2	All sites
Nematoda			
Capillaria carbonis Rudolphi, 1819	0.53 ± 0.03	1.3 ± 0.1	All sites
Contracaecum rudolphii Hartwich, 1964	0.29 ± 0.03	0.7 ± 0.1	CI, LG, LL, LW, ML, LC, LG, WC, WL
Acanthocephala			
Polymorphidae	0.04 ± 0.01	0.09 ± 0.04	CI, LC, LG, WC

auritus and other cormorant species near sampling regions in this study (Dubois & Mahon, 1959; Hutton & Sogandares-Bernal, 1960; Hutton, 1964; Threlfall, 1982; Chandler & Rausch, 1984; Kuiken *et al.*, 1999; Overstreet & Curran, 2004, Robinson *et al.*, 2008, 2009; Doffitt *et al.*, 2009; Dronen, 2009; Violante-Gonzalez *et al.*, 2011; Garcia-Varela *et al.*, 2012; Wagner *et al.*, 2012; O'Hear *et al.*, 2014; Kudlai *et al.*, 2015) and confirm the widespread distribution of many parasites of this host. In particular, *D. auritus* occurred in all locations sampled in this study, consistent with high prevalence values reported in Robinson *et al.* (2010) and Wagner *et al.* (2012). This is also the first report of *Echinochasmus* sp. in *P. auritus* in the United States. Additionally, the widespread frequency (present at 100% of localities sampled) of tapeworm infections of *P. auritus* is revealed. Although identification of cestodes to species from frozen *P. auritus* was unsuccessful, we suggest that this is a previously underrepresented parasite group in cormorants and additional studies on unfrozen host samples could help elucidate their identities and distributions.

The high variety of parasites found in *P. auritus* confirms the generalist feeding habits of this waterbird, with over 250 fish species documented in its range (Dorr *et al.*, 2014b). Shared parasites among sampling localities and between seasons suggest that the life cycles of many parasites of *P. auritus* persist throughout the range

of their definitive host. This could result from a lack of intermediate host specificity or from infections in widely distributed intermediate hosts, such as the bullhead (*Ameiurus* sp.), gizzard shad (*Dorosoma cepedianum*) and yellow perch (*Perca flavescens*), and first intermediate hosts, such as mollusc and arthropod congeners (Holl, 1932; Arnold, 1934; Thomas, 1937; Krueger, 1954; Carney & Dick, 2000; Poulin & Dick, 2007). Alternatively, infection durations that persist through multiple seasons could explain the similarities between wintering and breeding parasite communities. This possibility is particularly intriguing because interspecific interactions among parasites could exclude (competition) or promote (facilitation) parasites that are expanding in range (Lello *et al.*, 2004; Johnson & Buller, 2011) through changes in definitive host distribution. Despite overall similarities in parasite infracommunity composition, we were able to detect significant differences of host sex and seasonality using parasite richness and diversity metrics.

We expected parasite diversity to be higher in immature birds collected on the breeding grounds and found instead that their parasite infracommunity diversities were no different from those of breeding adults. Rather than expanding their foraging territory, it appears that immature birds forage with groups of breeding adults and remain close to nest sites, despite their ability to spend a larger proportion of their time travelling to and acquiring

Table 4. Model output from generalized linear models (GZMs) testing for differences in age and breeding status, where sample group is a random variable in both mixed models. Three GZMs tested for differences in parasite intensity (abundance), species richness and diversity (exp(Shannon)) for both predictor groups. The two right-hand columns show the mean and standard error for the groups tested in each model.

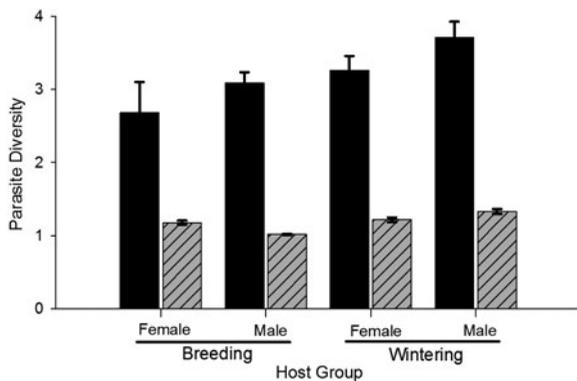| Model parameters	Response	χ^2	*P* value	Immature	Mature
Age, sample(random)	Abundance	0.049	0.824	36.9 ± 7.6	41.0 ± 6.7
	Richness	0.259	0.611	3.1 ± .2	2.7 ± .1
	exp(Shannon)	0.053	0.818	0.6 ± 0.1	0.4 ± 0.1
				Breeding	Wintering
Breeding status, sample(random)	Abundance	0.421	0.517	58 ± 9	14 ± 14
	Richness	5.111	0.024	3.0 ± 0.1	3.4 ± 0.1
	exp(Shannon)	17.384	< 0.001	1.8 ± 0.1	2.2 ± 0.1

Fig. 1. Species richness (filled bars) and diversity (hatched bars) of intestinal helminths from female and male *P. auritus* collected on breeding and wintering grounds. The models for species richness ($P < 0.01$, $\chi^2 = 14.4$, Overdispersion = 0.45) and Shannon Diversity ($P < 0.01$, $\chi^2 = 12.8$, Overdispersion = 0.03) indicated significant differences between breeding and wintering birds and between sexes, but not the interaction of season and sex.

food. This hypothesis is supported by the findings of Dorr *et al.* (2016), who reported that about 20% of cormorants collected from foraging flocks near breeding colonies were non-breeding birds. Consequently, future parasitological studies of *P. auritus* need not focus on particular age classes of this host.

There were differences in parasite assemblages between male and female *P. auritus* during the breeding and wintering seasons. Despite shared brooding and provisioning responsibilities, it appears that foraging behaviour and diets of breeding male and female *P. auritus* differ. Differences in foraging behaviour between sexes has been documented on the breeding and wintering grounds. Anderson *et al.* (2004) reported that males were more likely to forage at night and encounter a distinct prey/parasite assemblage. Additionally, foraging depth and duration can differ between the sexes of foraging waterbirds (Casaux *et al.*, 2001). We observed provisioning of *P. auritus* partners during incubation (K.L. Sheehan, Clemson University, pers. obs.), suggesting that foraging and feeding between parents could be more asymmetrical than previously reported. Similarly, Dorr *et al.* (2014b) reported geographic segregation of sexes on the wintering grounds in cormorants, presumably influenced by sex-specific prey and habitat preferences. Differences in parasite communities among cormorants on the wintering grounds, where males forage more frequently at aquaculture facilities than females (Craig *et al.*, 2016), were expected. Despite increased use of catfish aquaculture, the results here suggest that male *P. auritus* feed on a similar diversity of food items as female cormorants, and that supplemental feeding on farmed fish increases cormorant parasite infracommunity richness. Future studies of culled cormorants should make a similar effort to obtain large sample sizes of both sexes, a difficult task as morphological differences are not consistent between male and female cormorants.

Distinct diversities of parasites between breeding and wintering birds were detected even when locality and temporal replications were accounted for. This pattern of increased diversity in wintering birds could indicate that birds in winter forage in habitats with higher diversities of intermediate host species. If true, parasite infracommunity diversity within definitive hosts could be a useful indicator for targeted biodiversity sampling of intermediate host communities. Alternatively, the differences in parasite diversity between breeding and wintering birds could represent the variety of habitats where hosts forage. Other researchers have documented vast foraging ranges of *P. auritus* on the wintering grounds compared to those of breeding birds (King, 1996; Custer & Bunck, 1992; Coleman *et al.*, 2005; Dorr *et al.*, 2012). Although further verification of foraging habits should be conducted on tagged birds, our data suggest that as foraging range increases, parasite richness and diversity also increase.

Here we have successfully identified differences in the composition of intestinal parasite infracommunities, despite limitations in identifying some parasite groups because of frozen specimen preservation. Richness and diversity of parasites in *P. auritus* differ between male and female hosts and between seasons. Although differences in host maturity are not represented in their parasite infracommunities, a more complete representation of richness with identification of cestode species could change these results. We suggest that parasites are an integrative indicator of not only temporal diet, but also of foraging range (Dorr *et al.*, 2012). The parasites infecting *P. auritus* are acquired when birds forage on fish prey, and can indicate dominant food sources of piscivorous birds in the wild. The parasites of cormorants can help identify colonies that are a nuisance to aquaculture, habitats where predator deterrence should be employed to manage natural resources, and foraging grounds where they are less likely to compete with humans for fisheries resources. Consequently, parasites should be considered as ecological indicators of host behaviour and distribution, particularly for species that are subject to management as a consequence of human–wildlife conflicts.

Conflict of interest

None.

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