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# Physiological impacts of sublethal *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus* infections in captive Lesser Scaup (*Aythya affinis*)

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## ABSTRACT

Thousands of Lesser Scaup (*Aythya affinis*) die annually in the Upper Mississippi River System, USA, from intestinal infections after birds consume exotic faucet snails, *Bithynia tentaculata*, infected with introduced parasites, *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus*. To date, the low frequency (biannual) and magnitude of mortality events from intestinal infections likely prevents trematode mortalities from being a major contributor to Lesser Scaup population declines. However, questions remain regarding the role sublethal infections may have on Lesser Scaup fitness along with the potential for carryover effects in the following breeding season. We examined the impact of a single sublethal *C. bushiensis* and *S. pseudoglobulus* infection on select physiological parameters in Lesser Scaup over a 10-day period post inoculation through three trials, each involving three experimental groups: baseline control, trial control, and treatment ( $n = 96$  scaup). We found that male Lesser Scaup that were in better body condition before the trial had fewer *C. bushiensis* and *Sphaeridiotrema pseudoglobulus* recovered from their intestines at necropsy. Individuals with the highest numbers of *C. bushiensis* and *S. pseudoglobulus* in their intestines lost the largest amounts of body mass during the trial. We found that blood urea nitrogen and triglycerides were lower when *C. bushiensis* and *S. pseudoglobulus* were present. Triglycerides and glucose declined from Day 0 to Day 5 but stabilized on Day 10 of the trial. Our results highlight changes in physiological metrics in Lesser Scaup from a sublethal infection with *C. bushiensis* and *S. pseudoglobulus* under experimental conditions. Changes in Lesser Scaup health parameters indicated that scaup surviving a single sublethal trematode infection may have reduced body condition, which could lead to negative health implications in the following breeding season.

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## Impactos fisiológicos de infecciones subletales por los tremátodos *Cyathocotyle bushiensis* y *Sphaeridiotrema pseudoglobulus* en patos *Aythya affinis* cautivos

### RESUMEN

Miles de patos *Aythya affinis* mueren anualmente en el sistema fluvial del Upper Mississippi River, EUA, por infecciones intestinales después de que estas aves consumen los caracoles *Bithynia tentaculata* exóticos infectados con los parásitos introducidos *Cyathocotyle bushiensis* y *Sphaeridiotrema pseudoglobulus*. A la fecha, la baja frecuencia (bianual) y la magnitud de los eventos de mortandad como consecuencia de infecciones intestinales, posiblemente evita que las muertes por trematodos representen una contribución mayor a los declives poblacionales de este pato. Sin embargo, quedan preguntas acerca del papel que las infecciones subletales podrían tener en el fitness de *Aythya affinis*, así como el potencial efecto de acarreo en la siguiente temporada reproductiva. Examinamos el impacto de una única infección subletal de *C. bushiensis* y *S. pseudoglobulus* en algunos parámetros fisiológicos en este pato en un periodo de 10 días posinoculación a través de tres ensayos, cada uno compuesto por tres grupos experimentales: línea-base control, ensayo control y tratamiento ( $n=96$  patos). Encontramos que los machos que estaban en mejor condición corporal antes del experimento tenían menos *C. bushiensis* y *Sphaeridiotrema pseudoglobulus* recuperados de sus intestinos durante su necropsia. Los individuos con las mayores cantidades de ambos trematodos en sus intestinos perdieron la mayor cantidad de masa corporal durante el experimento. Encontramos que el nitrógeno ureico en sangre y los triglicéridos fueron menores cuando estaban presentes *C. bushiensis* y *S. pseudoglobulus*. Los triglicéridos y la glucosa declinaron del Día 0 al Día 5, pero se estabilizaron en el Día 10 del experimento. Nuestros resultados destacan cambios en las métricas fisiológicas en *Aythya affinis* como consecuencia de infecciones subletales de *C. bushiensis* y *S. pseudoglobulus* bajo condiciones experimentales. Los cambios en los parámetros de salud en *Aythya affinis* indican que los patos que sobreviven infecciones por estos trematodos podrían tener una condición corporal disminuida, lo cual podría tener implicaciones negativas para su salud en la siguiente temporada reproductiva.

*Cyathocotyle bushiensis*, *Sphaeridiotrema globulus*, and *S. pseudoglobulus* are trematodes that cause recurrent mortality events in North American waterfowl and waterbirds (~22,000 waterfowl and other waterbirds died from trematode infections in 2006; Sauer et al. 2007). The faucet snail, *Bithynia tentaculata*, is the first and second intermediate host of *C. bushiensis* and *S. pseudoglobulus* (Cole and Franson 2006; Herrmann and Sorensen 2011) and waterfowl and other waterbirds are the definitive host in the Upper Mississippi River System, USA (i.e., Illinois, Iowa, Minnesota, and Wisconsin). The faucet snail, native to Europe, was introduced to North America in the 1870s (Mills et al. 1993). The introduced trematodes were first documented in North America in 1928 (i.e., *Sphaeridiotrema globulus*; Price

1934) and 1961 (i.e., *C. bushiensis*; Gibson et al. 1972) and now occur in many freshwater systems throughout the Great Lakes region, the Upper Mississippi River System, and in isolated areas of Montana (Perez et al. 2016).

In the Upper Mississippi River System, trematode mortalities in waterbirds, mainly Lesser Scaup (*Aythya affinis*) and American Coot (*Fulica americana*) were observed starting in the early 2000s (Cole and Franson 2006; Sauer et al. 2007; WHISPers 2022). Trematodiasis and its related mortalities and morbidities (Sauer et al. 2007; Conservation Breeding Specialist Group 2010; Herrmann and Sorensen 2011; England et al. 2018) is one of a wider suite of threats to scaup populations, which include wetland disturbance and degradation (Austin et al. 2000; Anteau and Afton 2008a), poor water quality (Walsh et al. 2006), reduced food availability (Afton and Anderson 2001), and increased competition with fish for food resources (Strand et al. 2008).

The spring condition hypothesis posits that a major factor contributing to Lesser Scaup population declines is female scaup reaching breeding grounds in reduced body condition due to less food and lower habitat quality at wintering and spring migration stopovers, which has subsequent negative impacts on recruitment (Anteau and Afton 2006). This hypothesis did not originally include factors such as infections with *C. bushiensis* and *S. pseudoglobulus* that could impact scaup overall health and body condition (Anteau and Afton 2006; England et al. 2018). Hunter-harvested scaup have trended toward a declining age ratio (more hatch year than adult) and an increasing male-biased sex ratio (more males than females), suggesting that adult female scaup survival may be declining (Padding et al. 2005; Raftovich et al. 2020). England et al. (2018) found scaup health was poorer in lower quality habitat and where *C. bushiensis* and *S. pseudoglobulus* abundance was higher, suggesting the trematodes could compromise female body condition and subsequent breeding success.

The helminth communities occurring in the Upper Mississippi River System have long infected migrating scaup (England et al. 2018). However, the addition of non-native snails as hosts of *C. bushiensis* and *S. pseudoglobulus* combined with reduced scaup habitat quality and quantity may have additive negative impacts on the body condition of scaup during spring migration. The magnitude of effects from sublethal infections of *C. bushiensis* and *S. pseudoglobulus* on Lesser Scaup population dynamics, while unknown, is of concern as faucet snails are predicted to spread farther south from the current extent of their North American range (i.e., Navigational Pool 13 in the Mississippi River). Establishment of snails and the trematodes at important scaup migration stopover sites, such as Navigational Pool 19 in the Mississippi River (Havera 1999; Anteau and Afton 2009; Austin 2010; Osborn et al. 2016) where mollusks are a major food source for refueling during spring migration (Thompson 1973; Larson 2021), could have a significant effect on migrating scaup.

Given the changes in vegetation and food communities on major river pools in the last half century (Moore et al. 2010; Stafford et al. 2010), food-borne infections could pose an additional and substantial risk for Lesser Scaup. Our objectives in this paper were to explore the effects of trematode infections on Lesser Scaup by evaluating (1) changes in selected clinical measures of health, (2) demographic factors, and (3) body condition during sublethal experimental infections with *C. bushiensis* and *S. pseudoglobulus*. We predicted that sublethal infections would alter clinical blood values and body condition as compared with uninfected control birds and in a negative manner in female scaup.

## Methods

### *Bird capture and husbandry*

Our work was conducted at the Forbes Biological Station (Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign) near Havana, Illinois, USA (40.29806, -90.06179), between March 2019 and October 2020. Lesser Scaup were captured in the Illinois River floodplain near Havana, Illinois, in March of 2019 and 2020. Additionally, captive-reared Lesser Scaup were hatched from eggs collected from nests of wild birds near Devils Lake, North Dakota, USA (48.03765, -98.94713), in June 2019.

### *Faucet snails*

Faucet snails were collected on 1–2 June 2019, 22 September 2019, and 21 September 2020 by hand, using long handled nets, or Ponar dredges from shallow, rocky areas in Navigation Pools 7 and 8 of the Mississippi River near La Crosse, Wisconsin. The U.S. Fish and Wildlife Service (USFWS) has reported annual avian mortalities due to intestinal trematodiasis caused by *C. bushiensis* and *S. pseudoglobulus* in these pools since 2000 (USFWS 2017).

Based on the average number ( $\bar{x} = 5$ ) of metacercariae per snail (Rebecca A. Cole, U.S. Geological Survey, National Wildlife Health Center, unpublished data), we collected >2,500 snails (~80 snails/bird) for each trial, to ensure approximately 200–400 metacercariae in each dose for use in infection trials. The target of 200–400 metacercariae was set at a predicted sublethal level and based on the total abundance of *C. bushiensis* and *S. pseudoglobulus* in apparently healthy, free-ranging scaup ( $\bar{x} = 258$ –454; England et al. 2018) and previous work by Huffman and Roscoe (1989) and Gagnon et al. (1993).

### *Metacercariae*

To prepare each dose, within 48 h of infection trials, snails were pulverized using a mortar and pestle and artificially digested (2 g pepsin and 3 mL of 12 M HCL in 200 mL distilled water) at 37°C for 15 min using a magnetic stirrer (Gagnon et al. 1993). The remaining sediment was washed through a 125  $\mu$ m sieve using tap water to remove digest solution (Hoeve and Scott 1988). We estimated the mean dose by counting an aliquot of the solution containing metacercariae prior to each trial using a dissecting microscope as reported by Khan (1962). Samples used to establish the mean dose were not administered to birds.

Metacercariae were identified to *C. bushiensis* or *Sphaeridiotrema* spp. via morphological characteristics reported by Khan (1962) and Szidat (1937). Sequencing of a portion of the cytochrome oxidase subunit 1 (CO1) (Van Steenkiste et al. 2015) from a subsample of metacercariae and subsequent subsample of adult worms recovered at necropsy verified identity as *S. pseudoglobulus*. Metacercariae used in infection trials were stored separately in Locke's solution at 4°C until infection (Gagnon et al. 1993).

### *Infection trials*

We initiated trials on Day 0 when birds were weighed, had their body temperature and an initial blood sample taken (details are shown in the following sections), and the infection

group received metacercariae via oral gavage. On Day 5 and 10, all infection and trial control birds were weighed and a second and third blood sample collected, respectively. On Day 0, the baseline control birds were euthanized, and on Day 10, all infection and trial control birds were euthanized. Details of the carcass dissection are covered in the following section.

**Trial 1**

In Trial 1 (Jul 2019, 4 months post-capture), we assigned wild-caught, after-hatch year female Lesser Scaup into three groups (baseline control, trial control, and treatment) using a stratified random design, with stratification based on the body condition index (mass/wing chord) (Johnson et al. 1985). Lacking a body condition index validated against body composition metrics for Lesser Scaup, we assumed this traditional index was reasonable for our purposes (Klimas et al. 2020). We assigned 8 birds to baseline control, 8 to trial control, and 21 to the treatment group (Table 1). For Trial 1, we only used female scaup, given that the spring condition hypothesis of population decline is focused on the body condition of females.

**Trial 2**

In this trial (Dec 2019, 7 months after hatching), we assigned captive-reared, hatch-year Lesser Scaup into three groups (i.e., baseline control, trial control, and treatment) using a stratified random design based on sex to ensure that a nearly even amount of male and female birds were represented in each experimental group. We assigned 4 to the baseline control (2 males and 2 females), 4 to the trial control group (2 males and 2 females), and 16 to the treatment group (9 males and 7 females, Table 1). Starting with Trial 2, we included both male and female birds, in part due to not having enough females hatch from collected eggs to complete a whole trial, and to assess if there were differences between the sexes in the response to infection. The total sample size for this trial was dependent on the number of nests located and hatching rate of the eggs, which was outside the control of the authors.

**Table 1.** Trial, bird captive status, sex, treatment group, number of birds (n), mean number metacercariae given to each Lesser Scaup (*Aythya affinis*), and the ratio of *Sphaeridiotrema pseudoglobulus* to *Cyathocotyle bushiensis* given per bird for each experimental infection trial between July 2019 and October 2020.

Trial	Captive status	Sex	Treatment group	<i>n</i>	Mean metacercariae per dose ± SD	<i>Sphaeridiotrema pseudoglobulus</i> : <i>Cyathocotyle bushiensis</i>
1	Wild caught	Female	Baseline controls	8	–	–
			Trial controls	8	–	–
			Infection	21	266 ± 39	0.64 ± 0.10
2	Captive reared	Male	Baseline controls	2	–	–
			Trial controls	2	–	–
			Infection	9	418 ± 11	2.24 ± 0.14
		Female	Baseline controls	2	–	–
			Trial controls	2	–	–
			Infection	7	418 ± 11	2.24 ± 0.14
		3	Wild caught	Male	Baseline controls	3
Trial controls	3				–	–
Infection	10				331 ± 24	1.21 ± 0.20
Female	Baseline controls			3	–	–
	Trial controls			3	–	–
	Infection			13	331 ± 24	1.21 ± 0.20

### **Trial 3**

In our third trial (Oct 2020, 7 months post capture), we assigned wild-caught, after-hatch-year Lesser Scaup into three groups (i.e., baseline control, trial control, and treatment) using a stratified random design based on sex to ensure that an approximately even number of male and female birds were represented in each treatment group. We initially planned to conduct this trial 4 months post capture as in Trial 1 but were delayed in response to workplace changes due to COVID-19 restrictions. We assigned 6 scaup to the baseline control group (3 males, 3 females), 6 to the trial control group (3 males, 3 females), and 23 to the treatment group (10 males, 13 females; Table 1).

### **Health evaluation, tissue collection, and carcass processing**

#### **Blood sampling and body temperature**

Body temperature was measured by inserting a thermometer into the cloaca of the bird on Day 0, 5, and 10 before blood sampling. To collect a blood sample, the medial metatarsal was cleaned with an alcohol swab, then a 2 mL blood sample was collected from the medial metatarsal vein using a 23-gauge needle. Total blood volume collected during each trial was no more than 2% of the total body weight, with no more than 0.4% total body weight collected at one time (Arsnoe et al. 2011). Within 30 min of each blood collection, plasma was separated from cellular components using a microcentrifuge (Basix™, Fisher Scientific, Waltham, Massachusetts) at 1,500 rpm for 10 min.

Plasma was pipetted into 2 mL sterile cryovials (Thermo Scientific™, Fisher Scientific, Waltham, Massachusetts) and stored frozen until analyzed by clinical pathology staff at the College of Veterinary Medicine, University of Illinois Urbana Champaign for  $\beta$ -hydroxybutyrate, non-esterified fatty acids, triglycerides, blood urea nitrogen, glucose, eosinophil, basophils, monocytes, bilirubin, and albumin using a Beckman Coulter AU680 Chemistry Analyzer and Beckman Coulter reagents (Beckman Coulter, Brea, California). Packed cell volume (PCV) was determined in duplicate from 70  $\mu$ L of fresh, whole blood collected into heparinized microhematocrit tubes (Fisherbrand™, Fisher Scientific, Waltham, Massachusetts). Ratio of blood cells to volume was measured using a Leica Microsystems Covidien Microhematocrit Tube Reader (Fisher Scientific, Waltham, Massachusetts).

#### **Carcass processing**

Each bird was weighed to the nearest 1 g prior to euthanasia. After euthanasia the abdominal cavity was exposed by peeling away the skin and cutting the ribcage enabling it to be pushed aside (England et al. 2018). The right liver lobe was obtained from each bird and frozen. The bill, feet, and feathers were removed from each bird and percent fat, moisture, protein, and ash of each carcass were determined via proximate analysis conducted following the procedures of Klimas et al. (2020).

To determine the number of adult *C. bushiensis* and *S. pseudoglobulus* in the gastrointestinal tract, the esophagus was closed with butcher's twine just posterior to the gizzard. The small intestine was then segmented into five equal sections from the gizzard to the ceca bifurcation using the twine. All sections of the intestinal tract were frozen in 70% non-denatured ethanol until examination.



For examination, both ceca were thawed, placed in separate dishes, opened longitudinally, and flushed with tap water. Using a dissecting scope, *C. bushiensis* and *S. pseudoglobulus* adults were counted, removed, and preserved in 70% non-denatured ethanol. The quantity of trematode eggs was estimated on a clear Petri dish using a 10, 50, or 100 egg unit count similar to aerial waterfowl surveys (Gilbert et al. 2021). Following the removal of parasites, all plaques and cores from each cecal mucosa were removed, dried for 24–48 h in a drying oven, and weighed separately (Hoeve and Scott 1988). The same procedure was conducted on each section of the small intestine and the colon cloacal section. The terms abundance, intensity, and prevalence are used herein as reported by Bush et al. (1997).

### **Statistical analyses**

All model sets described in the following section were compared using Akaike's Information Criterion (AIC). We interpreted the top model results from variables with beta-coefficients ( $\beta$ -estimates) with 85% confidence limits that did not overlap zero (Arnold 2010). All data analysis was completed in R version 4.3.3 (R Core Team 2023).

#### **Body condition pre-trial, sex, and dosage impacts on trematode abundance**

Impact of baseline body condition, infection dosage (low in Trial 1 and high in Trials 2 and 3), and sex on total trematode abundance, was evaluated by employing a generalized linear model with *C. bushiensis* and *S. pseudoglobulus* abundance as the response variable. This analysis included the data from all three trials and only included data from the infection treatment group. We developed an *a priori* set of models that included an overall (all variables) and null (intercept-only) model (Supplemental Table S1).

#### **Infection impacts on mass change over the trial**

To evaluate the impact of trematode infection on Lesser Scaup body condition during trials, we used a general linear model with the difference between body mass on Day 10 and Day 0 as the response variable and sex, treatment (control and infection), infection dosage (low in Trial 1 and high in Trials 2 and 3), total cecal core weight, and average percent fat of carcasses and *C. bushiensis* and *S. pseudoglobulus* abundance as predictor variables. We developed an *a priori* set of models that included an overall (all variables) and null (intercept-only) model (Supplemental Table S2).

#### **Physiological response to infection treatment**

To evaluate physiological responses to infection during trials, we used a generalized mixed-effect model with bird identity as a random effect to account for the repeated measures. We made *a priori* predictions about the impact of each physiological response variable (Table 2). This analysis included the data from all three trials and only included data from the trial control and infected treatment groups. We used each variable in Table 2 as a response variable for its own model set. The same set of *a priori* candidate models were used in each model set that included an overall (all variables) and null (intercept-only) model.



**Table 2.** Physiological response variables, with corresponding units, and our predicted relationship of each variable over time to *Sphaeridiotrema pseudoglobulus* and *Cyathocotyle bushiensis* infection trial in Lesser Scaup (*Aythya affinis*) in captivity.

Response variable	Units	Predicted relationship over time in trial	Relationship over time in trial
Temperature	°C	Increase	No relationship
Eosinophils	%	Increase	Increase
Albumin	g/dL	Decrease	No relationship
Pack Cell Volume	%	Decrease	Decrease
Blood Urea Nitrogen	mg/dL	Increase	No relationship
Non-esterified fatty acids	mg/L	Increase	No relationship
Glucose	mg/dL	Increase	Decrease
$\beta$ -Hydroxybutyrate	mmol/L	Increase	No relationship
Triglycerides	mg/dL	Decrease	Decrease
Bilirubin	mg/dL	Increase	No relationship
Monocytes	%	Increase	No relationship
Basophils	%	Increase	Increase

**Results**

**Infection loads**

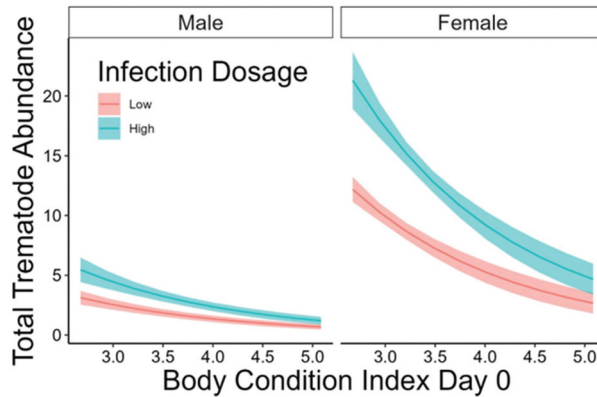
An estimated 260–420 *C. bushiensis* and *S. pseudoglobulus* metacercariae were administered to each treatment duck on Day 0 of infection trials (Table 1). The prevalence of trematode infection was 57.1% for Trial 1 (Table 3). In Trial 1, more ducks were infected with *S. pseudoglobulus* than *C. bushiensis*. The prevalence of trematode infection was 68.7% for Trial 2 (Table 1). In Trial 2, more scaup were infected with *C. bushiensis* than *S. pseudoglobulus* (Table 3). The prevalence of trematode infection was 85% for Trial 3 (Table 1). In Trial 3, more ducks were infected with *S. pseudoglobulus* than *C. bushiensis* (Table 3).

**Body condition pre-trial, sex, and dosage impacts on trematode abundance**

The top model included all the predictor variables (Supplemental Table S1). There was a negative relationship between body condition on Day 0 and *C. bushiensis* and *S. pseudoglobulus* abundance ( $\beta = -0.63$ , 85% CI =  $[-0.85 - -0.41]$ , Fig. 1). On average, male Lesser Scaup had fewer *C. bushiensis* and *S. pseudoglobulus* than females ( $\beta = -1.36$ , 85% CI =  $[-1.58 - -1.14]$ ). Lower trematode dosage resulted in lower *C. bushiensis* and *S. pseudoglobulus* abundance ( $\beta = -0.55$ , 85% CI =  $[-0.71 - -0.40]$ ).

**Table 3.** Number of Lesser Scaup (*Aythya affinis*) in experimental infection trials between July 2019 and October 2020 that received doses of trematode metacercariae that had adult trematodes in their digestive tracts upon dissection 10 days later.

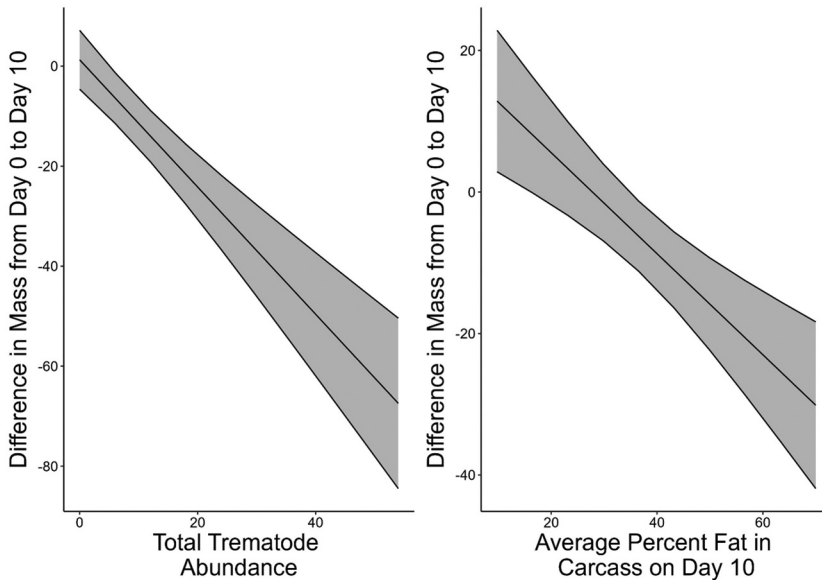
Trial	Sex	Sample size	Dose	Number birds infected	Number with <i>Cyathocotyle bushiensis</i>	Number with <i>Sphaeridiotrema pseudoglobulus</i>	Number with both
1	Female	21	200–400	12	2	12	2
2	Female	7	200–400	5	5	3	3
2	Male	9	200–400	6	6	3	3
3	Female	11	200–400	9	4	9	4
3	Male	9	200–400	8	5	5	2



**Figure 1.** Relationship between Lesser Scaup (*Aythya affinis*) body condition (higher values are better body condition) at the start of an infection trial and abundance of the trematodes *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus* in the intestines of scaup at necropsy. Shaded area represents the 85% confidence interval.

### *Infection impacts on mass change over the trial*

The top model included sex, total trematode abundance (at necropsy) and percent fat from the carcass (Supplemental Table S2). We found no difference between male and female scaup since the 85% CI overlapped zero ( $\beta = -7.8$ , 85% CI =  $[-21.6 - 5.81]$ ). Ducks with higher total trematode abundance had greater mass loss over the trial ( $\beta = -1.2$ , 85% CI =  $[-1.7 - -0.75]$ , Fig. 2); those with more percent fat in the carcass had greater mass loss over the trial ( $\beta = -0.7$ , 85% CI =  $[-1.17 - -0.25]$ ).

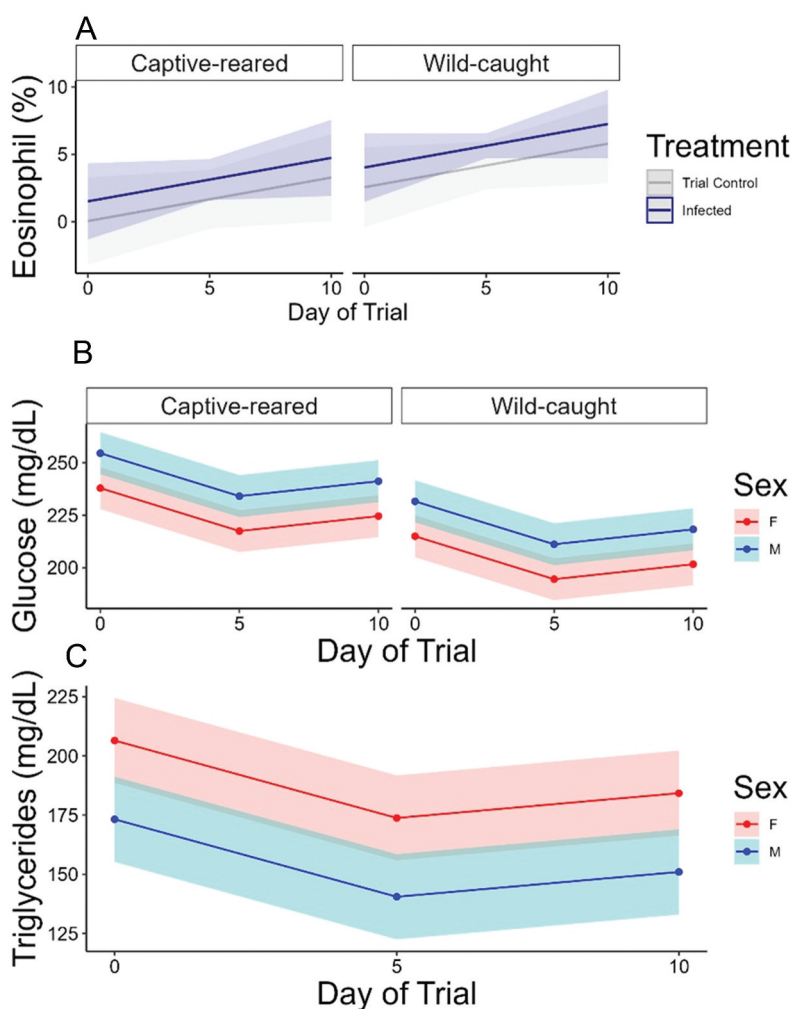


**Figure 2.** Mass difference across the 10 day trial by (left) total trematode abundance in the intestines of Lesser Scaup (*Aythya affinis*) that underwent experimental infections of *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus* and (right) average percent fat in carcass on Day 10. The shaded area represents the 85% confidence interval.

### Physiological response to infection over time

Supplemental Table S3 provides summaries of each blood value by treatment, trial day, and sex. The intercept-only model was the top model or within 2  $\Delta$ AIC of the top model for body temperature, albumin, non-esterified fatty acids, and bilirubin (Supplemental Tables S4–S7). Table 2 provides an overview of the different physiological response variables, the predicted relationship, and the relationship we found, with more details on individual physiological response model results in the following paragraphs.

The trial day + source + treatment model was the highest ranked for eosinophils (Supplemental Table S8). Eosinophils increased from Day 0 to Day 10 in the trial ( $\beta = 0.40$ , 85% CI = [0.30–0.50], Fig. 3). Wild-caught birds had more eosinophils than



**Figure 3.** Eosinophils (A), glucose (B), and triglycerides (C) across days of the trial from Lesser Scaup (*Aythya affinis*) that underwent experimental infections of *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus*.

captive-reared birds ( $\beta = 3.0$ , 85% CI = [1.98–4.11], Fig. 3). Infected birds had higher eosinophils than trial control birds ( $\beta = 1.80$ , 85% CI = [0.63 – 2.98], Fig. 3).

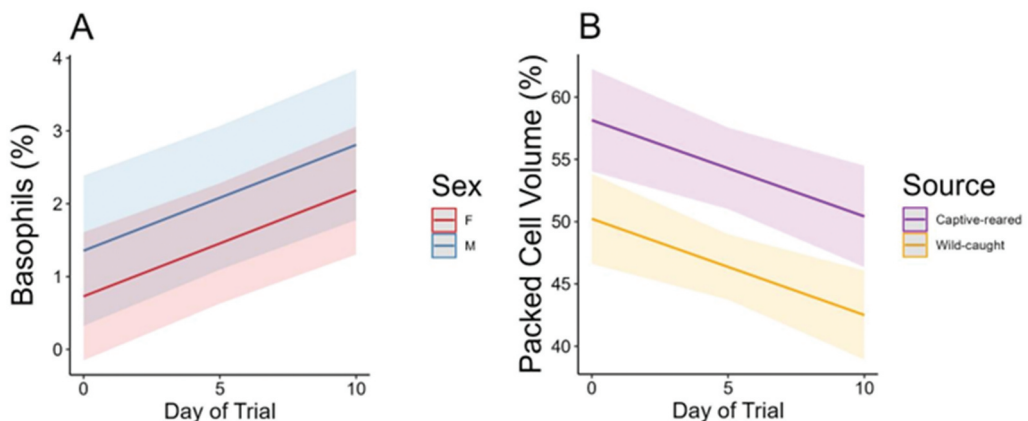
The trial day + source + treatment model was the highest ranked for PCV (Supplemental Table S9). Packed cell volume decreased from Day 0 to Day 10 of the trial ( $\beta = -0.43$ , 85% CI = [-0.53 – -0.33], Fig. 4). Wild-caught birds had lower packed cell volume than captive-reared birds ( $\beta = -7.51$ , 85% CI = [-9.07 – -5.95], Fig. 4). We did not find a difference in PCV between the treatment and trial control birds.

The trematode presence + source + treatment model was the highest ranked for blood urea nitrogen (Supplemental Table S10). Blood urea nitrogen was lower when trematodes were present ( $\beta = -1.32$ , 85% CI = [-2.29 – -0.36], Fig. 5). Wild-caught birds had higher blood urea nitrogen than captive-reared birds ( $\beta = 1.79$ , 85% CI = [0.91–2.67]). We did not find a difference in blood urea nitrogen between the treatment and trial control birds.

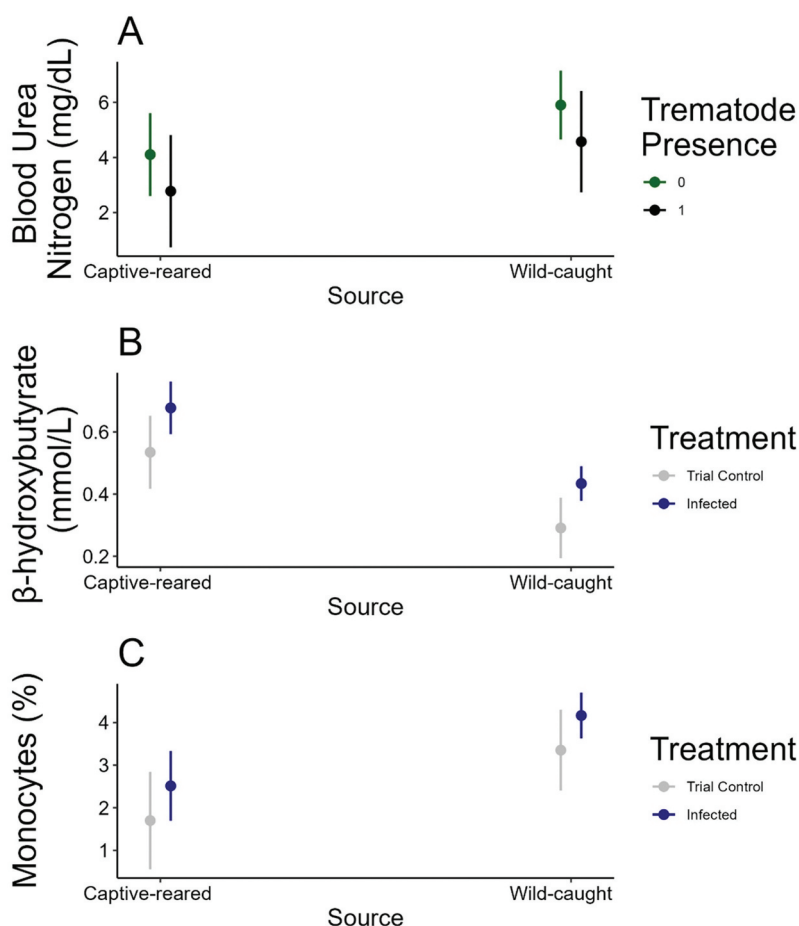
The highest ranked model for glucose was the overall model (Supplemental Table S11). We found a quadratic relationship with glucose over time, where glucose decreased from Day 0 to Day 5 and then increased from Day 5 to Day 10 ( $\beta = -6.84$ , 85% CI = [-9.57 – -4.12],  $\beta = 0.55$ , 85% CI = [0.29, 0.81], Fig. 3). Glucose was higher in males than females ( $\beta = 16.61$ , 85% CI = [7.04–26.18]) and lower in wild-caught birds ( $\beta = -22.91$ , 85% CI = [-32.67 – -13.14]). We did not find a difference in glucose based on *C. bushiensis* or *S. pseudoglobulus* presence between infected and trial control birds.

The source and treatment model for  $\beta$ -hydroxybutyrate was the highest ranked model (Supplemental Table S12). We found that wild-caught scaup had lower  $\beta$ -hydroxybutyrate than captive-reared ducks ( $\beta = -0.24$ , 85% CI = [-0.32 – -0.16], Fig. 5). Infected scaup had higher  $\beta$ -hydroxybutyrate than trial controls ( $\beta = 0.14$ , 85% CI = [0.06–0.21]).

The overall model for triglycerides was the highest ranked (Supplemental Table S13). We found triglycerides had a quadratic relationship, where they declined from Day 0 to Day 5 and then increased from Day 5 to Day 10 ( $\beta = -10.87$ , 85% CI = [-13.93 – -7.81];  $\beta = 0.86$ , 85% CI = [0.57 – 1.15], Fig. 3). Males had lower triglycerides than females ( $\beta = -33.30$ , 85% CI = [-50.03 – -16.55]). Triglycerides were lower when *C. bushiensis* or *S. pseudoglobulus* were present ( $\beta = -24.17$ , 85% CI = [-42.04 – -6.30]). We did not find a difference in triglycerides between wild caught and captive raised birds, or between infected and trial control birds.



**Figure 4.** Basophils (A) and Packed Cell Volume (B) across days of the trial of Lesser Scaup (*Aythya affinis*) experimentally exposed to *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus*.



**Figure 5.** Blood Urea Nitrogen (A),  $\beta$ -hydroxybutyrate (B), and Monocytes (C) among sources of Lesser Scaup (*Aythya affinis*) that underwent experimental infections of *Cyathocotyle bushiensis* and *Sphaeridiotrema pseudoglobulus*.

The source and treatment model for monocytes was the highest ranked model (Supplemental Table S14). Wild-caught scaup had higher monocytes than captive-reared scaup ( $\beta = 1.65$ , 85% CI = [0.98 – 2.34], Fig. 5). Treatment birds had higher monocytes than trial controls ( $\beta = 0.81$ , 85% CI = [0.07–1.55]). The highest ranked model for basophils was day of trial + sex + treatment (Supplemental Table S15). We found that basophils increased over the trial ( $\beta = 0.10$ , 85% CI = [0.10–0.18], Fig. 4). Males had higher basophils compared to females ( $\beta = 0.62$ , 85% CI = [0.05–1.19]). We did not find a difference in basophils between treatment and trial control birds.

## Discussion

The spring condition hypothesis of scaup population decline posits that female scaup reach the breeding grounds in reduced body condition due to poor habitat quality and lack of food during spring migration, which may be leading to lower reproductive success (Anteau

and Afton 2004). Reduced habitat quality at spring-stopover sites, including reduced availability of preferred amphipod food resources, may be driving Lesser Scaup to consume more gastropods, including *B. tentaculata* (Anteau and Afton 2006, 2008a). While *C. bushiensis* and *S. pseudoglobulus* are known to play a role in direct mortality of scaup and other waterbirds (Cole and Franson 2006; Sauer et al. 2007; Herrmann and Sorensen 2011), we aimed to evaluate the physiological response of single exposure, nonlethal infection loads on scaup in captivity. Our results support previous field studies that demonstrated that sublethal infections by *C. bushiensis* and *S. pseudoglobulus* could further reduce body condition of infected scaup while at stopover sites during spring migration, but the mechanisms are complex (England et al. 2018). Stored energetic resources can increase a bird's ability to initiate immune response, survive inappetence, and survive tissue destruction from infection (Marteinson et al. 2017).

We found that Lesser Scaup in better body condition prior to dosing experienced reduced trematode infection intensity. While all individuals lost mass during trials, reduced trematode infection intensity at necropsy was correlated with decreased mass loss. Being in better body condition might allow scaup to better respond to trematode infections, but it did not completely mitigate the effects of infection. Infected female scaup exhibited greater trematode abundance than males, and birds with greater trematode abundances lost greater amounts of body mass during trials. For spring migrating female scaup, trematode infections could further reduce body condition and increase cross-seasonal effects caused by poor habitat quality and lower food availability implicated by Anteau and Afton (2004) in the spring condition hypothesis.

Higher hemic  $\beta$ -hydroxybutyrate and triglyceride levels are indicative of short-term lipid catabolism and accumulation, respectively, in birds (Anteau and Afton 2008b; Smith et al. 2021; Bouton et al. 2023). We found greater  $\beta$ -hydroxybutyrate levels and lower triglyceride levels in infected scaup suggesting that even though food was available *ad libitum* (Beach et al. 2024), infected birds metabolized lipid reserves to supplement poor nutrient absorption due to the trematode induced intestinal mucosal damage or reduced food consumption rates while fighting the infection. Parasite infections can often induce inappetence (Mrugała et al. 2023) and interfere with processing of food (Hoste 2001; Mrugała et al. 2023). Triglyceride levels were lowest on Day 5 corresponding with the onset of reproduction in adult trematodes (Khan 1962; McLaughlin et al. 1993). Triglycerides were slightly higher by Day 10, when adult trematodes senesce (Berntzen and Macy 1969), which may have led to increased feeding, increased nutrient absorption from foods by scaup, or both. While we did not find a change in blood urea nitrogen over time, it was lower when *C. bushiensis* and *S. pseudoglobulus* were present, suggesting that trematode infection may have also caused birds to feed less, birds were unable to assimilate protein from the feed, or both.

Although we predicted that scaup inoculated with *C. bushiensis* and *S. pseudoglobulus* would exhibit altered clinical blood values and body condition as compared to uninfected control birds, only  $\beta$ -hydroxybutyrate, monocytes, and eosinophils varied between treatment groups. Increased levels of  $\beta$ -hydroxybutyrate in infected scaup are intuitive because birds may have been more likely to mobilize lipids in response to nutrient malabsorption or inappetence, and/or to fuel immune response. Monocytes are white blood cells and part of innate immunity that responds to foreign bodies including helminths. Increased

percentages of these cells found in the infected group were indicative of an immune response. Eosinophil levels will increase in direct response to helminth infections but also act as a control agent for other immune cell types and tissue damage (McLaren 1980).

We did not find a difference in body temperature, albumin, non-esterified fatty acids, and bilirubin between control and infected scaup. Our findings differ from Gagnon et al. (1993) who found that body temperature and cecal cores both increased with infection. Lower levels of blood urea nitrogen in scaup with adult trematodes may have been caused by decreased liver function, acute starvation, or severe bacterial infections following infection (Fiorello 2020). Lower triglycerides in scaup with trematodes indicate these scaup were using energy in response to infections and did not have extra energy resources to mobilize into lipid storage.

Based on England et al. (2018) and expected responses to trematode infection, we predicted trends of physiological response during the 10-day trial. As predicted, PCV decreased during the trials likely because of blood loss from damage to the small intestine from attachment and feeding by the trematodes and fluid loss due to *C. bushiensis* attachment and destruction of the cecal mucosa (Erasmus et al. 1963; Huffman and Roscoe 1989).

We expected glucose levels to increase but instead found that levels decreased on Day 5 and increased slightly on Day 10. Glucose levels remained within the clinical range (Sweazea 2022) and may have been elevated at the beginning of the trial as a stress response to being handled (Vagasi et al. 2020; Beach et al. 2024). We predicted an increase in monocytes during the study because of their role in responding to foreign bodies via phagocytosis, and the process of immune cell mobilization, defense, and digestion of foreign substances (Turgeon 2005). However, monocyte percentages remained unchanged during the trials. England et al. (2018) found basophils were positively associated with infection intensity of *C. bushiensis* and consistent with our prediction we found an increase in basophils over the days of the trial, but no difference between control and treatment birds. Basophils are another white blood cell response to foreign bodies and can increase vascular permeability that can facilitate the introduction of other white blood cells to the site of injury (Maxwell and Robertson 1995).

Previous work on trematode communities from scaup collected in the wild found negative relationships between trematode abundance and blood concentrations of non-esterified fatty acids and albumin (England et al. 2018). However, we found no such relationship in our work. Experimental birds were infected once while migratory wild birds were most likely exposed and infected continually while migrating through pools with *B. tentaculata*. Baseline stress levels, nutrient intake, activities such as foraging, and other factors likely varied substantially between wild and captive birds, which could lead to differing physiological responses. We note that captive birds were maintained on a consistent diet ration *ad libitum* that may have improved body condition and reduced ill-effects of nutrient limitation (England et al. 2018).

Our work was conducted on birds held in captivity, as that was required to experimentally infect them with trematodes and evaluate their physiological responses. Captive work introduces potential differences in physiology, but it is the only reasonable way to control other variables and introduce parasites experimentally (Beach et al. 2024). Given that metacercariae begin invading intestinal tissues within hours of ingestion and wild scaup naturally harbor numerous helminth species (Vest 2002; England et al. 2018), after-hatch-year scaup used in Trials 1 and 3 had likely been



exposed to diverse helminth communities during their migratory passage(s), including potential exposure to *C. bushiensis* and *S. pseudoglobulus*. There is evidence that prior infection of Canada Geese (*Branta canadensis*) and Mallards (*Anas platyrhynchos*) with sublethal dosages of *S. globulus* may lead to resistance to subsequent reinfections, even at otherwise lethal dosages (Huffman and Roscoe 1986, 1989). Trial 2 birds were hatched in captivity leaving them naïve to helminth exposure but also in greater body condition relative to formerly wild birds acclimated to captivity. In all three trials, birds were on a diet that met their nutritional needs, but that was not as diverse as those of wild birds. Other researchers (e.g., Gross et al. 2020; Smith et al. 2021; Bouton et al. 2023; Beach et al. 2024) have dealt with similar issues associated with artificial diets but shown that ducks can still deposit nutrients and maintain body condition in captivity on artificial diets. Despite potential differences between wild and captive birds, this body of work, including three experimental trials under different conditions and England et al.'s (2018) work with wild scaup, suggests a linkage between bird health and trematodiasis.

If anything has become clear, it is that the relationship between wetland conditions, foods, parasites, and bird condition is complex and natural system variability likely interacts in ways that are challenging to control and predict. Generally, waterfowl are resilient, though substantial variation exists among individuals and between species in infection susceptibility (Hoeve and Scott 1988). As we saw in this study, some individuals likely have few issues recovering from trematodiasis whereas others suffer mortality or chronic direct or indirect health effects from infection. Our study provides an important foundation for future work to better understand the impacts of sublethal infections on wild scaup populations.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

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## Ethics statement

All handling and captive holding protocols were approved by the Institutional Animal Care and Use Committee at University of Illinois at Urbana-Champaign and Western Illinois University (Protocol #18128 and #009–20, respectively); the U.S. Fish and Wildlife Service (#MB145466-3, #MB145466-4, and #MB145466-6); Illinois Department of Natural Resources (#W19.6079 and #W20.6079A); and North Dakota Game and Fish Department (Permit #GNF04969331).

## Statement on the use of AI

AI was not used in any form in this work.

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