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Seasonal Occurrence and Community Structure of Helminth Parasites in Green Frogs, *Rana clamitans melanota*, from Southeastern Wisconsin, U.S.A.

MATTHEW G. BOLEK[1] AND JAMES R. COGGINS

Department of Biological Sciences, University of Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201, U.S.A. (e-mail: coggins@csd.uwm.edu)

ABSTRACT: From April to October 1996, 75 green frogs, *Rana clamitans melanota*, were collected from Waukesha County, Wisconsin, U.S.A. and examined for helminth parasites. Seventy-one (94%) of 75 green frogs were infected with 1 or more helminth species. The component community consisted of 12 species: 5 trematodes, 2 cestodes, and 5 nematodes. Approximately 2,790 (72%) trematodes, 447 (11.5%) cestodes, and 636 (16.5%) nematodes were found. A significant correlation existed between wet weight and helminth species richness. Helminth populations and communities were seasonally variable and/or did not show significant differences during the year. *Haematoloechus varioplexus* showed seasonal variation in size during the year that was related to recruitment period. The helminth fauna of green frogs was depauperate and dominated by indirect-life-cycle parasites. Host diet and aquatic habitat were important in the transmission dynamics of these species. Host size, sex, and time of collection were also important factors in structuring helminth communities of green frogs and may mask any simple explanations.

KEY WORDS: *Rana clamitans, Haematoloechus varioplexus, Halipegus eccentricus, Glypthelmins quieta, Cosmocercoides* sp., *Oswaldocruzia pipiens, Waltonella* sp., *Mesocestoides* sp., metacercariae, Trematoda, Nematoda, Cestoda, Amphibia, seasonal study, Wisconsin, U.S.A.

Studies by Kennedy et al. (1986) on freshwater fish, birds, and a mammal have developed predictions in determining helminth community structure, particularly that ectotherm and endotherm helminth communities are fundamentally different: the former are species poor and noninteractive, while the latter are diverse and interactive. A review by Aho (1990) indicated that helminth communities of amphibians are highly variable, depauperate, and noninteractive in structure, but there is a need to examine and reexamine more species from different locations. To date there are few studies that utilized helminth community measures in amphibian hosts (Goater et al., 1987; Aho, 1990; Muzzall, 1991a, b; Goldberg et al., 1995; Barton, 1996; Yoder and Coggins, 1996; McAlpine, 1997; Bolek and Coggins, 2000). A number of helminth surveys of green frogs, *Rana clamitans melanota* Rafinesque, 1820, have been published (Campbell, 1968; Williams and Taft, 1980; Coggins and Sajdak, 1982; McAlpine and Burt, 1998), but there are few studies on the helminth infracommunity and component community structure of this species (Muzzall, 1991a; McAlpine, 1997), and none that incorporated a seasonal component.

Green frogs are large, semiaquatic frogs inhabiting freshwater ponds, lakes, swamps, and slow-moving streams in North America. They spend most of their time around the water's edge. They occur from Newfoundland to western Ontario, and south to eastern Oklahoma, southern Illinois, northern Georgia, and eastern North Carolina. In Wisconsin, these frogs overwinter buried in the mud and are active from early April through October (Vogt, 1981). Green frogs are largely sit-and-wait gape-limited predators, feeding on any accessible prey of appropriate size, including aerial, aquatic, and terrestrial invertebrates, primarily insects (Seale, 1987; Werner et al., 1995). Here we report on the seasonal helminth community structure of green frogs from southeastern Wisconsin. Specifically, we were interested in how host habitat, age and/or size, diet, sex, and seasonality were important in determining helminth populations and communities of green frogs.

Materials and Methods

A total of 75 green frogs, *R. clamitans melanota*, was collected from April to October 1996 at a small spring-fed permanent pond located at the Carroll College field station in Waukesha County, Wisconsin,

[1] Corresponding author. Current address: School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska 68588, U.S.A. (e-mail: mbolek@unlserve.unl.edu).

U.S.A. (42°59′N; 88°21′W). Ten to 15 frogs were collected monthly around the periphery of the pond by a dip-net. Animals were placed in plastic containers, transported to the laboratory, stored at 4°C, and euthanized in MS 222 (ethyl m-aminobenzoate methane sulfonic acid) within 72 hr of capture. Snout–vent length (SVL) and wet weight (WW) were recorded for each individual. Frogs were individually toe-clipped and frozen. At necropsy, the digestive tracts, limbs and body wall musculature, and internal organs were examined for helminth parasites. Each organ was placed individually in a petri dish and examined under a stereomicroscope. The body cavities were rinsed with distilled water into a petri dish and the contents examined. All individuals were sexed by gonad inspection during necropsy. Worms were removed and fixed in alcohol–formaldehyde–acetic acid or formalin. Trematodes and cestodes were stained with acetocarmine, dehydrated in a graded ethanol series, cleared in xylene, and mounted in Canada balsam. Nematodes were dehydrated to 70% ethanol, cleared in glycerol, and identified as temporary mounts. Prevalence, mean intensity, and abundance are according to Bush et al. (1997). Mean intensity was not calculated for the unidentified kidney metacercariae because they could not be counted accurately, and overall abundance was reported as an estimate of encysted metacercariae counted on the surface of the kidneys. Mean helminth species richness is the sum of helminth species per individual frog, including noninfected individuals, divided by the total sample size. All values are reported as the mean ± 1 standard deviation. Undigested stomach contents were identified to class or order following Borror et al. (1989). Stomach contents are reported as a percent = the number of prey items in a given class or order, divided by the total number of prey items recovered × 100. Voucher specimens have been deposited in the H. W. Manter Helminth Collection, University of Nebraska, Lincoln, Nebraska, U.S.A. (accession numbers HWML 15354, *Haematoloechus varioplexus* Stafford, 1902; 15355, *Glypthelmins quieta* Stafford, 1900; 15356, kidney metacercariae; 15357, *Mesocestoides* sp.; 15358, diplostomid metacercariae; 15359, *Halipegus eccentricus* Thomas, 1939; 15360, unidentified adult tapeworm; 15361, *Cosmocercoides* sp.; 15362, unidentified larval nematode; 15363, unidentified species of *Waltonella* Schacher, 1974; 15364, *Oswaldocruzia pipiens* Walton, 1929).

The chi-square test for independence was calculated to compare differences in prevalence among host sex. Yates' adjustment for continuity was used when sample sizes were low. A single-factor, independent-measures ANOVA and Scheffe's posthoc test were used to compare among seasonal differences in mean intensity and mean helminth species richness. When variances were heteroscedastic, the Kruskal–Wallis test and the Kolmogorov–Smirnov two-sample test were used. Student's *t*-test was used to compare differences in mean intensity and mean helminth species richness between sex of hosts. Approximate *t*-tests were calculated when variances were heteroscedastic (Sokal and Rohlf, 1981). Pearson's correlation was used to determine relationships among host SVL and WW and abundance of helminth parasites, excluding larval platyhelminths. Pearson's correlation was calculated for host SVL and WW and helminth species richness per individual frog. Because WW gave a stronger correlation than SVL in each case, it is the only parameter reported. Because of low sample size during certain collection periods, data were pooled on a bimonthly basis to form samples of 15–20 frogs per season. Larval helminths were not included in the seasonal analysis, because they can also accumulate throughout the amphibian's life and thus mask monthly recruitment dynamics in adult frogs.

Results

A total of 75 adult green frogs, 43 males and 32 females, was collected during April through October 1996. No significant difference existed in the number of male and female frogs collected throughout the year ($\chi^2 = 7.01$, $P > 0.05$). The overall means of SVL and WW of green frogs were 68.8 ± 10.8 mm (range 39.8–89.4 mm) and 35.8 ± 15.5 g (5.4–75.6 g), respectively. There was no significant difference in mean SVL ($t = 0.10$, $P > 0.05$) or mean WW ($t = 0.24$, $P > 0.05$) in male and female frogs. Stomach content analyses of green frogs revealed a broad range of aerial, terrestrial, and aquatic invertebrates. Sixteen different groups of invertebrates were recovered from stomach contents of green frogs, with coleopterans, gastropods, and diplopodans making up the largest percentage.

Seventy-one (94%) of 75 *R. clamitans melanota* were infected with helminth parasites. The component community consisted of 12 species (5 trematodes, 2 cestodes, and 5 nematodes). Of these, 8 have indirect life cycles, 1 has a direct life cycle, and the life cycles of 3 are unknown. Overall mean helminth abundance, excluding larval platyhelminths, was 16.5 ± 38 with most frog infracommunities having 10 or fewer worms. In terms of abundance, digeneans dominated adult helminth communities (61.5% of total adult helminths). Prevalence ranged from 80% for kidney metacercariae to 1.3% for an unidentified adult cestode, a filarid nematode of the genus *Waltonella,* and an unidentified encysted nematode. Values for overall prevalence, mean intensity, mean abundance, and total number of helminths recovered are summarized in Table 1.

Statistically significant differences in prevalence or mean intensity existed between male and female frogs for *H. varioplexus, H. eccentricus,* kidney metacercariae, and unidentified species of *Mesocestoides* Valunt, 1863 and *Cos-*

Table 1. Prevalence, mean intensity (MI), mean abundance (MA), and total helminths found in 75 specimens of *Rana clamitans melanota* in Wisconsin.

Species	Prevalence: number (%)	MI ± 1 SD (range)	MA ± 1 SD	Number of worms recovered	Location
Trematoda					
Haematoloechus varioplexus	33 (44)	5.3 ± 7 (1–30)	2.3 ± 5.4	176	Lungs
Halipegus eccentricus	17 (22.6)	1.9 ± 1.7 (1–8)	0.4 ± 1.1	33	Eustachian tubes
Glypthelmins quieta	11 (14.6)	35.5 ± 34.7 (1–110)	5.2 ± 18	391	Small intestine
Unidentified metacercariae*	60 (80)	NC‡	NC	>1,770	Kidneys, body cavity
Diplostomid metacercariae*	12 (16.0)	35 ± 41 (1–100)	5.7 ± 20.7	420	Leg muscles
Cestoda					
Unidentified adult cestode	1 (1.3)	1	0.01 ± 0.1	1	Small intestine
Mesocestoides sp.*	14 (18.6)	31.9 ± 22 (12–86)	5.9 ± 15.3	446	Leg muscles, lungs
Nematoda					
Oswaldocruzia pipiens	21 (28)	14.7 ± 23 (1–90)	4.1 ± 13.7	310	Small intestine, stomach
Cosmocercoides sp.	19 (25)	3.3 ± 4.3 (1–19)	0.8 ± 2.6	62	Large intestine, small intestine
Waltonella sp.†	1 (1.3)	4	0.05 ± 0.5	4	Body cavity
Larval nematode	9 (12)	25.9 ± 61 (1–200)	3.5 ± 23	259	Large intestine
Encysted nematode	1 (1.3)	1	0.01 ± 0.1	1	Small intestine

* Underestimate.
† New host record.
‡ Not counted.

mocercoides Harwood, 1930 (Table 2). Both *H. varioplexus,* a lung trematode, and *H. eccentricus,* a trematode of the eustachian tubes, had significantly higher mean intensities in male frogs, while the kidney metacercariae occurred at a higher prevalence in males. Female frogs had significantly higher mean intensities of *Mesocestoides* sp. and *Cosmocercoides* sp.

Mean helminth species richness was 2.68 ± 1.29 species per frog. Infections with multiple species were common, with 0, 1, 2, 3, 4, and 5 species occurring in 4, 8, 23, 20, 13, and 7 frogs, respectively. No statistically significant differences in mean helminth species richness were found between male (2.76 ± 1.01) and female frogs (2.56 ± 1.52, $t = 0.66$, $P > 0.05$). A nonsignificant positive correlation was found between overall helminth abundance, excluding larval platyhelminths, and WW ($r = 0.04$, $P > 0.05$). Nonsignificant relationships were also observed for most helminth species: unidentified adult cestode ($r = -0.01$, $P > 0.05$), *H. varioplexus* ($r = 0.10$, $P > 0.05$), *H. eccentricus* ($r = 0.19$, $P > 0.05$), *G. quieta* ($r = -0.02$, $P > 0.05$), *O. pipiens* ($r = -0.12$, $P > 0.05$), unidentified larval nematode ($r = -0.04$, $P > 0.05$), *Waltonella* sp. ($r = 0.20$, $P > 0.05$), and encysted nematodes ($r = -0.19$, $P > 0.05$). The nematode *Cosmocercoides* sp. had a significant positive correlation with WW ($r = 0.31$, $P < 0.01$). A significant positive Pearson's correlation also existed between species richness and WW ($r = 0.31$, $P < 0.01$). However, correlations between frog WW and species richness were not significant in May–June ($r = 0.31$, $P > 0.05$), July–August ($r = 0.01$, $P > 0.05$), and September–October ($r = 0.29$, $P > 0.05$) but were significant for the April collection ($r = 0.60$, $P < 0.02$).

The trematodes *H. varioplexus* and *H. eccentricus* occurred throughout the year, with highest prevalences observed during the fall (September–October) collection, 65% and 30%, respectively. The intestinal trematode, *G. quieta,* was

Table 2. Prevalence (Pr) and mean intensity (MI) of helminth parasites in male and female green frogs, *Rana clamitans melanota*.

Species	Measure of parasitism	Males $N = 43$	Females $N = 32$	Statistic	P
Trematoda					
Haematoloechus varioplexus	Pr	46.5 (20/43)	40.6 (13/32)	$\chi^2 = 0.24$	>0.05
	MI ± 1 SD	7 ± 8.6	2.8 ± 2.2	$t'_s = 3.07$	<0.05
Halipegus eccentricus	Pr	23.3 (10/43)	21.9 (7/32)	$\chi^2 = 0.02$	>0.05
	MI ± 1 SD	2.3 ± 2.1	1.4 ± 0.5	$t'_s = 2.71$	<0.05
Glypthelmins quieta	Pr	11.6 (5/43)	18.8 (6/32)	$\chi^2 = 0.46$	>0.05
	MI ± 1 SD	21.8 ± 27.9	47 ± 38.1	$t = 1.35$	>0.05
Unidentified metacercariae*	Pr	90.7 (39/43)	65.6 (21/32)	$\chi^2 = 5.72$	<0.05
	MI ± 1 SD	NC‡	NC		
Diplostomid metacercariae*	Pr	18.6 (8/43)	12.5 (4/32)	$\chi^2_{adj} = 0.16$	>0.05
	MI ± 1 SD	45.3 ± 46.1	14.5 ± 23.7	$t = 1.23$	>0.05
Cestoda					
Unidentified adult cestode	Pr	2.3 (1/43)	0 (0/32)	$\chi^2_{adj} = 0.02$	>0.05
	MI ± 1 SD	1	0		
Mesocestoides sp.*	Pr	23.3 (10/43)	12.5 (4/32)	$\chi^2_{adj} = 0.78$	>0.05
	MI ± 1 SD	24.9 ± 16.2	49.3 ± 24.8	$t = 6.69$	<0.05
Nematoda					
Oswaldocruzia pipiens	Pr	27.9 (12/43)	28.1 (9/32)	$\chi^2 = 0.00$	>0.05
	MI ± 1 SD	16.6 ± 25.8	12.2 ± 19.6	$t = 0.44$	>0.05
Cosmocercoides sp.	Pr	20.9 (9/43)	31.3 (10/32)	$\chi^2 = 1.00$	>0.05
	MI ± 1 SD	2 ± 1.7	4.4 ± 5.6	$t'_s = 3.81$	<0.05
Waltonella sp.	Pr	0 (0/43)	3.1 (1/32)	$\chi^2_{adj} = 0.02$	>0.05
	MI ± 1 SD	0	4		
Larval nematode	Pr	9.3 (4/43)	18.8 (6/32)	$\chi^2_{adj} = 1.67$	>0.05
	MI ± 1 SD	11.5 ± 11.2	35.5 ± 80.6	$t'_s = 1.67$	>0.05
Encysted nematode	Pr	0 (0/43)	3.1 (1/32)	$\chi^2_{adj} = 0.02$	>0.05
	MI ± 1 SD	0	1		

* Underestimate.
‡ Not counted.

first observed during midspring (May–June) with a prevalence of 5%. Prevalence for this species reached its maximum (30%) during summer (July–August) and decreased during the fall collection (20%). Seasonal mean intensity of adult platyhelminths followed similar patterns as prevalence, but no significant differences existed for any of the adult platyhelminths recovered, *H. eccentricus* (adjusted $H = 2.02$, $P > 0.05$), *H. varioplexus* ($F = 0.34$, $P > 0.05$), or *G. quieta* ($t = 0.43$, $P > 0.05$).

Although prevalence and intensity of *H. varioplexus* did not vary significantly throughout the collection period, mean length of worms did (Fig. 1). Greatest mean length of worms (4.1 mm) was recorded in early spring (April), when all individuals were gravid adults, and reached a minimum during midspring (1.84 mm), when immature individuals were common. Statistically significant differences in mean length were observed for April and May–June collections, April and July–August collections, May–June and September–October collections, and July–August and September–October collections ($F = 11.8$, $P < 0.05$, single-factor, independent-measure ANOVA; $P < 0.05$ for all pair-wise comparisons, Scheffe's test).

The nematodes *Waltonella* sp. and an unidentified encysted larva were recovered infrequently as single infections during midspring and fall collections, respectively. Prevalence and intensity values for *O. pipiens, Cosmocercoides* sp., and unidentified larval nematodes were low and/or erratic over the 7-mo period. The nematodes *O. pipiens, Cosmocercoides* sp., and unidentified larval nematodes were first observed during midspring and persisted until fall, with prevalence being highest in summer for *O. pipiens* (62%) and midspring and summer for *Cosmocercoides* sp. (40%) and larval nematodes (20%). However, only *O. pipiens* exhibited statistically significant differences (adjusted $H =$

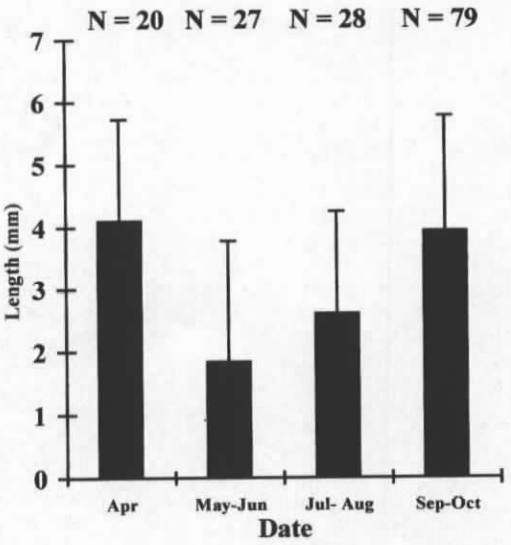

Figure 1. Mean lengths of *Haematoloechus varioplexus* from *Rana clamitans melanota*. *N* = number of worms measured from all frogs recovered in each sampling period.

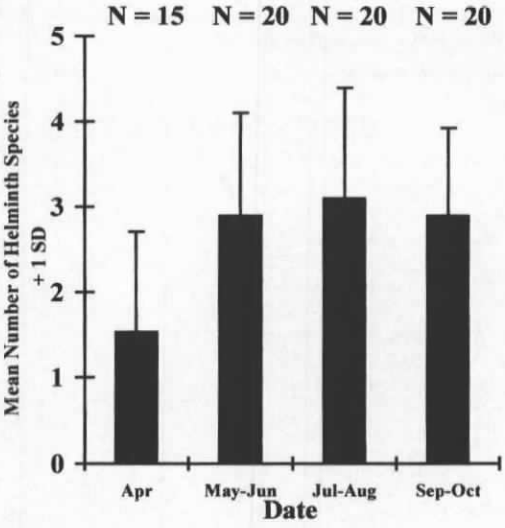

Figure 2. Mean helminth species richness of *Rana clamitans melanota* during April, May–June, July–August, and September–October 1996. *N* = number of frogs collected on each date.

9.45, $P < 0.05$) in mean intensity. The two-sample Kolmogorov–Smirnov test revealed significant differences in mean intensities during the May–June (27 ± 30) and July–August (9.8 ± 17) collections.

Mean helminth species richness fluctuated seasonally (Fig. 2) and was lowest (1.53) during early spring and highest (3.1) during the summer collections. Statistically significant differences in mean helminth species richness were observed for April and May–June collections, April and July–August collections, and April and September–October collections ($F = 6.01$, $P < 0.05$, single-factor, independent-measure ANOVA; $P < 0.05$ for all pairwise comparisons, Scheffe's test). No statistically significant differences in frog WW were observed during the year ($F = 0.37$, $P > 0.05$).

Discussion

Wisconsin green frogs had high overall helminth prevalence, with parasite infracommunities being dominated by indirect life-cycle parasites. Of the identified parasites, only 1 direct life-cycle nematode, *O. pipiens,* was present, with most helminth species displaying a prevalence below 50% and/or low mean intensities below 30.

Most green frogs contained identifiable stomach contents containing predominantly beetles, gastropods, and diplopods. In total, 16 different groups of terrestrial, aerial, and aquatic invertebrates comprised their stomach contents. These results appear similar to those of other investigators (Hamilton, 1948; Stewart and Sandison, 1972; McAlpine and Dilworth, 1989; Werner et al., 1995). Hamilton (1948) found that the principal foods of green frogs collected in New York, U.S.A. consisted of beetles, flies, and grasshoppers, with a total of 15 different items recovered from adult frogs and 20 different prey items recovered from various sized individuals.

The most common helminth recovered was an unidentified kidney metacercaria. This larval trematode had an overall prevalence of 80% and mean intensity of over 30 worms per frog. Four other digeneans were recovered from green frogs: a diplostomid metacercaria encysted in the musculature, and 3 adult trematodes: *H. varioplexus, H. eccentricus,* and *G. quieta.* Frogs become infected with *H. varioplexus,* a lung trematode, and *H. eccentricus,* a eustachian tube trematode, by eating infected odonates (Krull, 1931; Dronen, 1975, 1978; Wetzel and Esch, 1996). *Glypthelmins quieta,* a trematode of the small intestine, is acquired when frogs ingest prey such as tadpoles, frogs, and/or shed skin infected with metacercariae (Prudhoe and Bray, 1982). Therefore, diet was important in the

transmission dynamics of these 3 trematode species in this study.

Haematoloechus varioplexus and *H. eccentricus* were recovered from frogs throughout the year, increasing, although not significantly, in both prevalence and mean intensity during the fall collection. Recently, Wetzel and Esch (1997) have shown that the life span of *H. eccentricus* may be variable, with trematodes capable of maturing in as little as 1 wk and being lost the following week. Because of the small number of these flukes recovered in our study, little can be said about their recruitment throughout the year. Krull (1931) estimated that the life-span of *Haematoloechus medioplexus* Stafford, 1902, averaged 1 yr, while studies by Kennedy (1980) on species of *Haematoloechus* have shown that trematodes can reach full length in only 60 days. The size differences observed for *H. varioplexus* during the year (Fig. 1) may be significant in understanding recruitment of this species. The seasonal variation in length of *H. varioplexus* suggests that adult worms are lost during early spring and that new infections begin during midspring and continue throughout the year. These results are similar to those of Ward (1909), who observed lung flukes of *Rana pipiens* Schreber, 1782, being lost during breeding, and recruitment occurring throughout the year.

Two cestode species were recovered from green frogs during this study, the larval tetrathyridium of *Mesocestoides* sp. and a single specimen of an adult cestode that could not be identified because the scolex was lost. The complete life cycles of *Mesocestoides* spp. are currently unknown; however, a number of mammals, amphibians, and reptiles are known to serve as second intermediate hosts, while carnivorous mammals serve as definitive hosts. The tetrathyridian stage has been reported from a variety of mammals and reptiles but is rare in amphibians (McAllister and Conn, 1990). The life cycles of these 2 species of cestode are unknown, although frog diet may be important in their transmission dynamics.

Nematodes in the genus *Waltonella* typically are found in the body cavity of species of *Rana*. Adult worms release microfilaria into the bloodstream, and mosquitoes serve as vectors, infecting frogs while feeding (Witenberg and Gerichter, 1944). The only report of filarial worms in *R. clamitans* is of microfilaria recovered from 1 frog in Ontario, Canada (Barta and Desser, 1984). Therefore, *R. clamitans melanota* is apparently a new host record for *Waltonella* sp. (Esslinger, 1986; Baker, 1987). *Waltonella americana* was previously reported and described in Wisconsin leopard frogs by Walton (1929).

The nematode *Cosmocercoides* sp. was recovered from the large intestine of green frogs. Confusion exists in the literature on the identification of species of *Cosmocercoides* in amphibians and reptiles (Baker, 1987; Vanderburgh and Anderson, 1987). The major difference in species identification is the number of rosette papillae per subventral row in males, with male *Cosmocercoides dukae* Holl, 1928 (gastropod parasite) having 9–21 rosette papillae, averaging 13–14, and *C. variabilis* (amphibian parasite) having 15–25, averaging 20 or 21. Because of this overlap and the presence of only 5 damaged males out of 62 nematodes recovered, species identification was not possible. Interestingly, no worms were found in the lungs or body cavity of any green frogs, and *Cosmocercoides* sp. occurred in frogs in months when gastropods were commonly found in the stomach contents. We suspect that specimens of *Cosmocercoides* sp. recovered are *C. dukae,* although this cannot be confirmed.

Differential infection between host sex and prevalence or mean intensity was observed for a number of helminth species. Male frogs had a significantly higher prevalence of kidney metacercariae and significantly higher mean intensities of *H. varioplexus* and *H. eccentricus* than female frogs. Male green frogs are territorial during the breeding season and defend their aquatic breeding site from potential competitors (Martof, 1953; Oldham, 1967). Thus, unlike the females, they remain in the water for longer periods of time and may be exposed to cercariae of the kidney trematode for longer periods. Because males remain in a relatively small area of the pond during the breeding season, they may occur in a microhabitat conducive to becoming infected with digeneans. Recently, Wetzel and Esch (1997), in a seasonal study of *Halipegus occidualis* Stafford, 1905 and *H. eccentricus* in green frogs, suggested that certain areas of a pond may be "hot spots" for infection with digenetic trematodes. Therefore, male frogs in these "hot spots" may feed more often on emerging odonates containing metacercariae of species of *Haematoloechus* and *Halipegus,* ex-

plaining the higher mean intensities of these trematodes observed in male frogs (Wetzel and Esch, 1996).

Female frogs had significantly greater mean intensities of *Cosmocercoides* sp. and *Mesocestoides* sp. than males. Although *Cosmocercoides* sp. could not be identified to species, both *C. variabilis* and *C. dukae* occur in terrestrial habitats. Female frogs spend more time on the ground and have a higher probability of encountering these nematodes in a terrestrial habitat, either by skin-penetrating *C. variabilis* or by feeding on terrestrial mollusks, hosts for *C. dukae*. Unfortunately, nothing can be stated about the transmission dynamics of *Mesocestoides* sp., and no conclusions can be drawn from this difference. The observed differences in host sex are probably due to ecological differences in their habitat preference throughout the year.

Significant positive relationships between WW and species richness were observed in green frogs. In this study, frogs in the later collections had greater species richness than in early collections (Fig. 2); therefore, time of exposure was more important in developing richer helminth communities than was frog weight during the May–June, July–August, and September–October collections. This is supported by the results showing significant differences in species richness over time and nonsignificant correlations between WW and species richness. Observations linking higher species richness with larger host size have been reported in green frogs and other species of *Rana* by Muzzall (1991a) and McAlpine (1997). These investigators suggested that older individuals may have a longer exposure time and possess more surface area for colonization by skin-penetrating nematodes and digenean metacercariae. Also, larger frogs possess a greater gape size and may feed on larger, and a wider number, of intermediate hosts than smaller individuals. As in their studies, our data also support the island size hypothesis, which predicts that larger host individuals should support higher species richness than smaller individuals (Holmes and Price, 1986). McAlpine (1997) also stated that aspects of host ecology, such as diet and habitat, and parasite transmission may confound any simple relationship between the diversity of helminth communities and size of hosts. Data from the present study suggest that time of transmission may also have a similar confounding effect.

The depauperate helminth community structure of Carroll College green frogs was similar to the community structure of green frogs examined from Michigan, U.S.A. and New Brunswick, Canada by Muzzall (1991a) and McAlpine (1997), respectively. Of the 120 frogs examined from Michigan, 108 (90%) were infected with a total of 13 species of helminths (8 trematodes, 1 cestode, and 4 nematodes) while 164 of 234 (70.1%) green frogs examined from Canada were infected with 18 species of helminths (10 trematodes, 3 cestodes, and 5 nematodes). As in our study, in terms of abundance, digeneans dominated the adult helminth communities of frogs in Michigan (96.5%) and New Brunswick (60.8%), indicating that diet and a semiaquatic habitat were also important in structuring helminth communities dominated by indirect-life-cycle parasites at those locations. Similarly, in both of those studies, adult frogs had higher species richness than young-of-the-year individuals, indicating that size and/or age were also important in acquiring new species of helminths into the infracommunity of these hosts. Data from our study and the Michigan and New Brunswick frogs suggest that although helminth species composition, richness, and prevalence may be variable depending on collection site and the ecological factors influencing variation in life history traits in local populations at those locations, green frog helminth communities are dominated by digenetic trematodes acquired in a semiaquatic habitat and/or through the frogs' diet.

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