J. Parasitol., 89(4), 2003, pp. 673–680

HELMINTH COMMUNITY STRUCTURE OF SYMPATRIC EASTERN AMERICAN TOAD, *BUFO AMERICANUS AMERICANUS*, NORTHERN LEOPARD FROG, *RANA PIPIENS*, AND BLUE-SPOTTED SALAMANDER, *AMBYSTOMA LATERALE*, FROM SOUTHEASTERN WISCONSIN

Matthew G. Bolek* **and James R. Coggins**
Department of Biological Sciences, University of Wisconsin—Milwaukee, Milwaukee, Wisconsin 53201. *e-mail: mbolek@unlserve.unl.edu*

ABSTRACT: One-hundred twelve amphibians, including 51 blue-spotted salamanders, *Ambystoma laterale*, 30 eastern American toads, *Bufo americanus americanus*, and 31 northern leopard frogs, *Rana pipiens*, were collected during April–October 1996 from Waukesha County, Wisconsin and examined for helminth parasites. The helminth compound community of this amphibian assemblage consisted of at least 10 species: 9 in American toads, 8 in leopard frogs, and 3 in blue-spotted salamanders. American toads shared 7 species with leopard frogs, and 2 species occurred in all 3 host species. Although there was a high degree of helminth species overlap among these sympatric amphibians, statistically significant differences were found among host species and percent of indirect or direct–life cycle parasites of amphibian species individual component communities ($\chi^2 = 1{,}015$, $P < 0.001$). American toads had a higher relative abundance of nematodes, 59%, than larval cestodes, 31%, and larval and adult trematodes, 10%, whereas leopard frogs had a higher relative abundance of larval cestodes, 71.3%, and larval and adult trematodes, 25.3%, than nematodes 3.4%. This is related to ecological differences in habitat and dietary preferences between these 2 anuran species. Helminth communities of blue-spotted salamanders were depauperate and were dominated by larval trematodes, 94%, and few nematodes, 6%. Low helminth species richness in this host species is related to this salamander's relatively small host body size, smaller gape size, lower vagility, and more fossorial habitat preference than the other 2 anuran species. Adult leopard frogs and toads had significantly higher mean helminth species richness than metamorphs, but there was no significant difference in mean helminth species richness among adult and metamorph blue-spotted salamanders. Considering adult helminths, the low species richness and low vagility of caudatans as compared with anurans suggest that local factors may be more important in structuring caudatan helminth communities of salamanders than of anuran hosts. Helminth species infecting salamanders may be more clumped in their geographic distribution as compared with anurans, and the role of other hosts and their parasites at the compound community level may be important in structuring helminth communities of salamanders.

Helminth communities can be classified at a hierarchical level. An infracommunity includes all helminth infrapopulations within an individual host. The component parasite community includes all the infracommunities within a given host population, whereas the compound helminth community consists of all the helminth infracommunities within a community of hosts (Holmes and Price, 1986; Bush et al., 1997). The comprehensive review by Aho (1990) on amphibian helminth community structure indicates that helminth communities of amphibians are highly variable, depauperate, and noninteractive in structure, but there is a need to examine more species from different locations and conduct studies on multiple species at the compound community level. Several investigators have recognized the value of amphibian communities as excellent systems to examine ecological concepts at the compound community level. Interspecific variation in host diet, life history, and body size among sympatric species offer an excellent comparative approach to understanding how these factors influence community structure (Goater et al., 1987; Goldberg et al., 1995; McAlpine, 1997; Goldberg et al., 1998; Yoder, 1998; Barton, 1999; Goldberg et al., 2002). In Wisconsin, the eastern American toad, *Bufo americanus americanus* Holbrook 1836, northern leopard frog, *Rana pipiens* Schreber 1782, and blue-spotted salamander, *Ambystoma laterale* Hallowell 1856, occur sympatrically and represent good subjects for comparative studies on helminth community structure in amphibian hosts. American toads are large, thick-bodied terrestrial anurans and considered active foragers that are found around marshes, oak savannas, semiopen coniferous and deciduous forests, and agricultural areas. Northern leopard frogs are considered semiaquatic, ambush predators that use shallow water habitats but can be found at long distances from water. *Ambystoma laterale* is a small semifossorial species that inhabits deciduous and coniferous forests, from moist bottomlands to dry uplands. In southeastern Wisconsin blue-spotted salamanders are spring breeders that migrate to breeding ponds in late March or early April and are commonly found breeding along with leopard frogs and American toads (Vogt, 1981; Seale, 1987; Bolek, 1998). Although a number of studies on the parasites of these species exist from the Midwestern United States (Coggins and Sajdak, 1982; Muzzall and Schinderle, 1992; Bolek, 1997; Yoder, 1998; Gillilland and Muzzall, 1999; Bolek and Coggins, 2000, 2002), no study examines the component parasite communities of adult and metamorphs of these 3 species of amphibians. Because these 3 amphibian species vary in body size, habitat preference, and diet (Vogt, 1981; Bolek, 1997; Bolek and Coggins, 2000), we were interested in elucidating what role, if any, host habitat, age or size, and diet plays in determining helminth populations and communities of these Wisconsin amphibians. In addition, we were interested in comparing characteristics of helminth communities of this amphibian assemblage of salamanders and anurans with other studies on anurans and caudatan helminth communities.

MATERIALS AND METHODS

A total of 112 adult and metamorph amphibians of 3 species were collected during April–October of 1996 from an ephemeral pond located in Brookfield, Waukesha County, Wisconsin (43°03′N, 88°04′W). Included were 15 adult and 15 metamorph American toads, *B. a. americanus*, collected in April and July, 20 adult and 11 metamorph northern leopard frogs, *R. pipiens*, collected in April, October, and July 1996, and 31 adult and 20 metamorph blue-spotted salamanders, *A. laterale*,

Received 10 December 2002; revised 31 March 2003; accepted 1 April 2003.
* Present address: School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, Nebraska 68588.

collected during April, May, and August 1996. Animals were placed in plastic containers, transported to the laboratory, stored at 4 C, and killed in MS 222 (ethyl m-aminobenzoate methane sulfonic acid) within 48 hr of capture. Snout–vent length (SVL) and wet weight (WW) were recorded for each individual. Most amphibians were individually toe clipped and frozen, whereas some were necropsied fresh. At necropsy the digestive tract, limbs, body wall musculature, and internal organs were examined for helminth parasites. Each organ was placed in individual Petri dishes and examined under a stereomicroscope. The body cavity was rinsed with distilled water into a Petri dish and the contents examined. All individuals were sexed by gonad inspection during necropsy. Worms were removed, 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. Certain tissues containing metacestodes and metacercaria were removed and fixed in 10% formalin, embedded in Paraplast, sectioned at 7 μm, affixed to slides and stained with Harris' hematoxylin and eosin, and mounted in Canada balsam. Nematodes were dehydrated to 70% ethanol, cleared in glycerol, and identified as temporary mounts. Prevalence, mean intensity, and mean abundance are according to Bush et al. (1997). Mean helminth species richness is the sum of helminth species per individual amphibian, including noninfected individuals, divided by the total sample size. All values are reported as the mean ± 1 SD. Voucher specimens have been deposited in the H.W. Manter Parasitology Collection, University of Nebraska, Lincoln, Nebraska (accession numbers HWML 17644, *Haematoloechus varioplexus*; 17645, *Gorgoderina attenuata*; 17647, Echinostomatid metacercariae; 17646, *Fibricola* sp.; 17648, *Mesocestoides* sp.; 17642, *Oswaldocruzia pipiens*; 17641, *Cosmocercoides variabilis*; 17640 *Rhabdias americanus*; 17643, *Spiroxys* sp.).

The chi-square test for independence was calculated to compare differences in prevalence among different host species. Yates' adjustment for continuity was used when sample sizes were low. Because variances were heteroscedastic, the Kruskal–Wallis test and the Kolmogorov–Smirnov 2-sample test were used to compare differences in mean abundance and mean helminth species richness among different host species and host age. Student's *t*-test was used to compare differences in mean intensity and mean helminth species richness between adult and metamorph 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 amphibian. Because WW gave a stronger correlation than SVL in each case, the former is the only parameter reported.

RESULTS

The helminth compound community of this amphibian assemblage consisted of at least 10 species (Table I). Of these, 6 have indirect–life cycles, 3 have direct–life cycles, and the life cycle of 1 is unknown. Of the 30 toads examined, 23 (14 adult and 9 metamorph individuals, 76.7%) were infected with helminth parasites. The component community consisted of 9 helminth species: 1 larval cestode, 1 adult and 2 larval trematodes, and 5 nematodes. The overall mean helminth abundance, excluding larval platyhelminths, was 20.7 ± 48.95 worms per infracommunity (range = 0–189). The prevalence was highest for *R. americanus* and *Fibricola* sp. meso and metacercariae (40%) and lowest, 3.3%, for *H. varioplexus* (Table I). Significant differences in prevalence occurred between adult and metamorphosed toads, with metamorphosed toads being infected with only 2 species of larval trematodes (Table II). Mean helminth species richness was 1.97 ± 1.9 species per toad. Multiple species infections were common with 0, 1, 2, 3, 4, 5, and 6 species occurring in 7, 9, 5, 2, 3, 2, and 2 toads, respectively. Statistically significant differences occurred in mean helminth species richness between adult 3.2 ± 1.86 and metamorphs 0.73 ± 0.7 ($t'_s = 4.80$, $P < 0.001$). A positive nonsignificant correlation existed for WW and total helminth abundance, excluding larval platyhelminths ($r = 0.31$, $P > 0.05$). Similar results were obtained for commonly occurring helminth species *C. variabilis* ($r = 0.23$, $P > 0.05$), *O. pipiens* ($r = 0.32$, $P > 0.05$) and *R. americanus* ($r = 0.25$, $P > 0.05$). A positive significant relationship was found for WW and species richness ($r = 0.50$, $P < 0.01$).

Of the 31 northern leopard frogs examined, 20 adults and 9 metamorphs (93.5%) were infected with 1 or more species of parasite. The component community consisted of 8 helminth species, including 4 trematodes, 1 larval cestode, and 3 nematodes. Overall, mean helminth abundance, excluding larval platyhelminths, was 2.58 ± 4.03 (range = 1–14) worms per frog. Prevalence ranged from a high of 64.5% for *Fibricola* sp. meso and metacercariae to a low of 3.2% for an unidentified larval nematode. Mean intensity was highest for *Mesocestoides* sp., 89.2 ± 104 (Table I). Of the 8 helminth species recovered, only 2 species, both larval trematodes, occurred in metamorphs, whereas all 8 were present in adult frogs (Table II). Species richness was variable among individuals, averaging 2.3 ± 1.3 species per frog. Multiple species infections were fairly common, with 0, 1, 2, 3, 4, and 6 species occurring in 2, 7, 9, 8, 4, and 1 host, respectively. Adult leopard frogs had significantly higher numbers of species per individual (2.8 ± 1.2) than metamorphs (1.3 ± 0.8) ($t = 3.35$, $P < 0.01$). A positive nonsignificant correlation existed between WW and total helminth abundance, excluding larval platyhelminths ($r = 0.20$, $P > 0.05$), *O. pipiens* ($r = 0.15$, $P > 0.05$), *G. attenuata* ($r = 0.19$, $P > 0.05$), and *H. varioplexus* ($r = 0.24$, $P > 0.05$). A significant positive correlation was found between frog WW and helminth species richness ($r = 0.48$, $P < 0.01$).

The component community of blue-spotted salamanders consisted of 3 species. Thirty-five (68%) of 51 salamanders (18 adults and 17 metamorphs) were infected with at least 1 species of helminth. Prevalence and mean intensity were highest for echinostomatid metacercariae (47% and 24 ± 17) and generally low for *Cosmocercoides* sp. and *Spiroxys* sp. (Table I). Metamorphs were infected with echinostomatid metacercariae only, whereas adults possessed all 3 helminth species. Both prevalence and mean intensity of echinostomatid metacercariae were significantly higher in metamorphs than in adults (Table II). Echinostomatid metacercariae were located throughout the ventrolateral region of the kidney tissue but were also commonly found within the lumen of Bowman's capsule. Mean helminth species richness was low for this host species, being 0.75 ± 0.6 species per individual with 16 salamanders infected with 0, 33 salamanders infected with 1, and 1 salamander infected with 2 and 3 species, respectively. There was no significant difference in helminth species richness between adults, 0.67 ± 0.70, and metamorphs, 0.85 ± 0.36 ($t'_s = 1.01$, $P > 0.05$). A significant positive correlation occurred for WW and overall helminth abundance, excluding larval platyhelminths ($r = 0.43$, $P < 0.01$) and *Cosmocercoides* sp. ($r = 0.35$, $P < 0.01$), but the correlation was not significant for *Spiroxys* sp. ($r = 0.26$, $P > 0.05$). There was also no significant correlation between WW and species richness ($r = 0.07$, $P > 0.05$).

The Kruskal–Wallis 1-way analysis of variance revealed significant differences in WW, host age, and species (H = 99.22, $P < 0.001$). The Kolmogorov–Smirnov 2-sample tests showed

TABLE I. Pr%, MI, and MA of helminth parasites recovered from eastern American toads, *Bufo americanus americanus*, northern leopard frogs, *Rana pipiens*, and blue-spotted salamanders, *Ambystoma laterale*, from Southeastern Wisconsin.*

	Bufo americanus americanus (n = 30)			*Rana pipiens* (n = 31)			*Ambystoma laterale* (n = 51)			
Species	Pr (%)†	MI ± SD (Range)	MA ± SD	Pr (%)†	MI ± SD (Range)	MA ± SD	Pr (%)†	MI ± SD (Range)	MA ± SD	Location
Trematoda										
Haematoloechus varioplexus‡	1 (3.3)	1 (1)	0.03 ± 0.18	5 (16.1)	2.2 ± 1 (1–4)	0.4 ± 0.9	0 (0)	—	—	L
Gorgoderina attenuata‡	0 (0)	—	—	5 (16.1)	2.8 ± 2.4 (1–7)	0.5 ± 1.4	0 (0)	—	—	UB
Echinostomatid metacercariae‡§	9 (30)	7 ± 3.6 (3–13)	2.1 ± 3.8	13 (41.9)	13 ± 10.5 (6–39)	5.4 ± 9.3	24 (47)	24 ± 17 (8–68)	11 ± 17	K, BC
Fibricola sp.‡§	12 (40)	3.4 ± 1.8 (1–7)	1.4 ± 2.0	20 (64.5)	10.9 ± 7.8 (1–35)	7 ± 8.1	0 (0)	—	—	LM, BC
Cestoda										
Mesocestoides sp.‡§	5 (16.7)	66 ± 22.6 (39–93)	11 ± 26.4	13 (41.9)	89.2 ± 104 (12–378)	37.4 ± 79.6	0 (0)	—	—	LM, BC
Nematoda										
Oswaldocruzia pipiens‖	8 (26.7)	24.1 ± 18.2 (6–56)	6.4 ± 14.1	11 (35.5)	3.6 ± 4 (1–14)	1.3 ± 2.9	0 (0)	—	—	SI
Cosmocercoides variabilis‖	8 (26.7)	5.8 ± 4.8 (1–15)	1.5 ± 3.5	0 (0)	—	—	0 (0)	—		L, BC, LI
Cosmocercoides sp.	0 (0)	—	—	0 (0)	—	—	10 (19.60)	2.5 ± 2.12 (1–7)	0.49 ± 1.35	L, LI
Rhabdias americanus‖	12 (40)	31.7 ± 55.7 (1–189)	12.7 ± 37.7	0 (0)	—	—	0 (0)	—	—	L, BC
Spiroxys sp.‡	3 (10)	3 ± 2 (1–5)	0.3 ± 1.1	3 (9.7)	2.3 ± 0.6 (2–3)	0.2 ± 0.7	4 (7.8)	2.5 ± 2.3 (1–6)	0.2 ± 0.9	SI
Unidentified juvenile nematode‡	2 (6.7)	1 ± 0 (1)	0.06 ± 0.3	1 (3.2)	9 (9)	0.3 ± 1.6	0 (0)	—	—	LI

* BC = body cavity; K = kidneys; L = lungs; LI = large intestine; LM = leg muscles; MA = mean abundance; MI = mean intensity; Pr% = prevalence; SI = small intestine; UB = urinary bladder.
† Number (%) infected.
‡ Indirect–life cycle parasite.
§ Underestimate.
‖ Direct–life cycle parasite.

TABLE II. Pr% and MI of helminth parasites recovered from adult and metamorphosed eastern American toads, *Bufo americanus americanus*, northern leopard frogs, *Rana pipiens*, and blue-spotted salamanders, *Ambystoma laterale*, from Southeastern Wisconsin.*

Species	Measure of parasitism	*Bufo americanus americanus* Adult (n = 15)	*Bufo americanus americanus* Metamorph (n = 15)	*Rana pipiens* Adult (n = 20)	*Rana pipiens* Metamorph (n = 11)	*Ambystoma laterale* Adult (n = 31)	*Ambystoma laterale* Metamorph (n = 20)
Trematoda							
Haematoloechus varioplexus	Pr	6.7 (1/15)	0 (0/15)	25 (5/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	1	—	2.2 ± 1	—	—	—
Gorgoderina attenuata	Pr	0 (0/15)	0 (0/15)	25 (5/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	—	—	2.8 ± 2.4	—	—	—
Echinostomatid metacercariae†	Pr	20 (3/15)	40 (6/15)	35 (7/20)	54.5 (6/11)	22.6 (7/31)‡	85 (17/20)‡
	MI ± SD	10 ± 2.6	5.5 ± 3.6	9.3 ± 1.7	17.6 ± 14.6	12.6 ± 2.6§	28.1 ± 18.3§
Fibricola sp.†	Pr	46.6 (7/15)	33.3 (5/15)	55 (11/20)	81.8 (9/11)	0 (0/31)	0 (0/20)
	MI ± SD	3 ± 2.6	4 ± 2	10 ± 5.6	13 ± 10.3	—	—
Cestoda							
Mesocestoides sp.†	Pr	33 (5/15)	0 (0/15)	65 (13/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	66 ± 22.6	—	89 ± 104	—	—	—
Nematoda							
Oswaldocruzia pipiens	Pr	53.3 (8/15)	0 (0/15)	55 (11/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	24.1 ± 18.2	—	3.6 ± 4	—	—	—
Cosmocercoides variabilis	Pr	53.3 (8/15)	0 (0/15)	0 (0/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	5.8 ± 4.8	—	—	—	—	—
Cosmocercoides sp.	Pr	0 (0/15)	0 (0/15)	0 (0/20)	0 (0/11)	32.3 (10/31)	0 (0/20)
	MI ± SD	—	—	—	—	2.5 ± 2.1	—
Rhabdias americanus	Pr	80 (12/15)	0 (0/15)	0 (0/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	31.7 ± 55.7	—	—	—	—	—
Spiroxys sp.	Pr	20 (3/15)	0 (0/15)	15 (3/20)	0 (0/11)	12.9 (4/31)	(0/20)
	MI ± SD	3 ± 2		2.3 ± 0.6		2.5 ± 2.4	
Unidentified juvenile nematode	Pr	13.3 (2/15)	0 (0/15)	5 (1/20)	0 (0/11)	0 (0/31)	0 (0/20)
	MI ± SD	1 ± 0	—	9	—	—	—

* Pr% = prevalence; MI = mean intensity.
† Underestimate.
‡ Comparison among adults and metamorphs significantly different $\chi^2_{adj} = 16.58$, $P < 0.01$.
§ Comparison among adults and metamorphs significantly different $t'_s = 3.76$, $P < 0.05$.

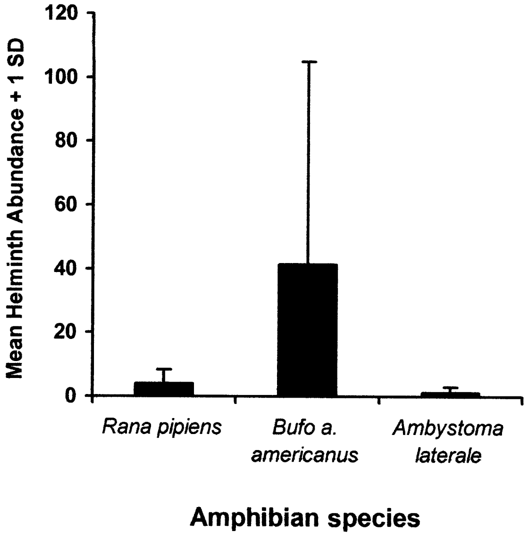

FIGURE 1. Mean helminth abundance, excluding larval plathyhelminths, among 3 species of adult amphibians.

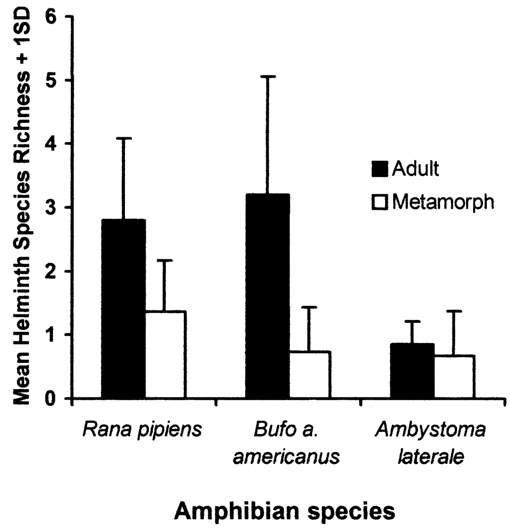

FIGURE 2. Mean helminth species richness among 3 species of adult and metamorph amphibians.

that all possible host species pairs differed significantly ($P < 0.05$) in WW except for the following combinations: adult *B. a. americanus* and adult *R. pipiens*, adult *A. laterale* and metamorph *R. pipiens*, and metamorph *A. laterale* and metamorph *B. a. americanus*. Adult *B. americanus* had the greatest weight (40.93 g $\pm$ 13.00) followed by adult *R. pipiens* (30.72 g $\pm$ 10.22), metamorph *R. pipiens* (3.95 g $\pm$ 1.24), adult *A. laterale* (3.15 g $\pm$ 1.03), metamorph *A. laterale* (0.38 g $\pm$ 0.11), and metamorph *B. a. americanus* (0.35 $\pm$ 0.09).

Significant differences also existed in overall prevalence between *R. pipiens*, 93.5%, and *A. laterale*, 68 %, ($\chi_{adj}^2 = 5.61$, $P < 0.05$), whereas no significant difference existed in overall prevalence between *R. pipiens* and *B. a. americanus*, 76.7% ($\chi_{adj}^2 = 2.22$, $P > 0.05$), or *B. a. americanus* and *A. laterale* ($\chi^2 = 0.6$, $P > 0.05$). The Kruskal–Wallis 1-way analysis of variance revealed significant differences in overall abundance ($H = 63.48$, $P < 0.001$, Fig. 1) and species richness ($H = 53.75$, $P < 0.001$, Fig. 2) among the 3 host groups and ages. The Kolmogorov–Smirnov 2-sample test revealed significant differences in helminth species richness in all possible host species pairs ($P < 0.05$) except for the following combinations: metamorph *A. laterale* and adult *A. laterale*, metamorph *B. a. americanus* and metamorph *A. laterale*, adult *B. a. americanus* and adult *R. pipiens*, metamorph *B. a. americanus* and adult *A. laterale*, and metamorph *B. a. americanus* and metamorph *R. pipiens*. The Kolmogorov–Smirnov 2-sample test also revealed significant differences in overall helminth abundance, excluding larval platyhelminths for all possible host species pairs ($P < 0.05$) except for the following combinations: metamorph *R. pipiens* and metamorph *A. laterale*, metamorph *R. pipiens* and adult *A. laterale*, metamorph *B. a. americanus* and metamorph *R. pipiens*, metamorph *B. a. americanus* and adult *A. laterale*, and metamorph *B. a. americanus* and metamorph *A. laterale*.

American toads had a higher relative abundance of nematodes, 59%, than larval cestodes, 31%, and larval and adult trematodes, 10%, whereas northern leopard frogs component helminth communities had a higher relative abundance of larval cestodes, 71.3%, and larval and adult trematodes, 25.3%, than nematodes, 3.4%. Component helminth communities of blue-spotted salamanders were dominated by larval trematodes, 94%, and few nematodes, 6%. Statistically significant differences were found for comparisons made among host species and percent of indirect or direct–life cycle parasites of individual amphibian species component communities ($\chi^2 = 1{,}015$, $P < 0.001$). Toads had a higher relative abundance of direct–life cycle nematodes, (58%), with 41.8% of the component community being indirect–life cycle parasites and 0.2% being unknown nematodes. Northern leopard frogs had a higher relative abundance of indirect–life cycle parasites, (96%), only 3% direct–life cycle parasites, and 1% unknown nematodes, whereas blue-spotted salamanders had more indirect–life cycle parasites, 95.8%, than unknown nematodes, 4.2%.

DISCUSSION

A number of studies on helminth parasites of northern leopard frogs, American toads, and blue-spotted salamanders exist (see Bolek, 1997; McAlpine, 1997; Gillilland and Muzzall, 1999; Bolek and Coggins, 2000). As in previous studies, the helminth communities of Wisconsin amphibians examined in this study were depauperate and isolationist in nature. Most helminth species did not show strict host specificity and have been reported in a range of amphibians (Prudhoe and Bray, 1982; Baker, 1987). American toads shared 7 species with leopard frogs, and blue-spotted salamanders shared 2 species with toads and leopard frogs (Table I). On average, individual hosts harbored 2 or fewer parasite species. Although host specificity cannot be ruled out, host habitat appeared to be important in structuring helminth communities in these amphibians. Semiaquatic, ambush predators such as northern leopard frogs were dominated by indirect–life cycle parasites associated with an aquatic habitat, or diet, or both, whereas active foragers such as American toads were more commonly infected with direct–life cycle skin-penetrating nematodes associated with their terrestrial habitat. The role of diet in structuring helminth communities of these amphibians probably reflects habitat differences and gape size of hosts examined. Terrestrial species such as American toads may feed less often on semiaquatic arthropods, which serve as intermediate hosts for trematode species, whereas semiaquatic, ambush predators such as northern leopard frogs may be exposed to such parasites more often. *Rana pipiens* may feed on numerous aquatic and semiaquatic insects and tadpoles or frogs that serve as intermediate hosts for trematodes such as *H. varioplexus* and *G. attenuata* (Krull, 1931; Rankin, 1939). Occurring in an aquatic habitat for a substantial part of the year may also have exposed these frogs to cercariae of larval trematodes. In contrast, adult toads only enter water for a short period to breed and feed predominantly on terrestrial arthropods during the year (Vogt, 1981; Bolek and Coggins 2000). Therefore, they are less likely to be exposed to parasites with aquatic life stages such as cercariae or metacercariae in intermediate hosts. These results support previous studies by Bolek and Coggins (2000, 2001) on the helminth community structure of amphibians and the role of habitat and diet of these hosts. They indicated that terrestrial anurans such as American toads were dominated by direct–life cycle skin-penetrating nematodes and semiaquatic green frogs, *Rana clamitans melanota*, were dominated by indirect–life cycle parasites that were acquired in an aquatic habitat, or through their diet, or both. Although we have no data to indicate which of the hosts sampled at our study site is the most abundant, results from this study suggest that at the compound community level adult and larval trematodes and larval cestodes cycle predominantly through semiaquatic ambush predators such as leopard frogs, whereas terrestrial toads acquire infection of these generalist helminths by similarities in diet and habitat preference.

Parasite component and infracommunities of blue-spotted salamanders were lower than for the anuran hosts examined in this study, with only 2 salamanders having concurrent infections of 2 or 3 helminth species. These differences may be attributed to anurans being bigger and exhibiting higher vagility than caudatans. Adult blue-spotted salamanders had significantly lower mean abundance and species richness than adult anurans. As stated by Muzzall (1991a), ''Frogs may occupy a number of habitats and feed on a wider variety of aerial, terrestrial and aquatic invertebrates than salamanders, contributing to a more diverse helminth fauna.'' This species differs in its biology from toads and leopard frogs. *Ambystoma laterale* is much smaller, more fossorial in habitat, has a smaller gape size and lower vagility, and, therefore, may not feed on aerial and semiaquatic insects that serve as hosts for digenetic trematodes as commonly as the other amphibians examined (Vogt, 1981). Bolek (1997) examined blue-spotted salamanders for helminth parasites and stomach content data and found that this species predominantly feeds on terrestrial and fossorial invertebrates. Therefore, the low species richness observed in this host may correspond to a smaller gape size and lower vagility. Also, because of their semifossorial habitat salamanders may not come into contact with skin-penetrating nematodes as commonly as the anuran hosts examined in this study.

Another reason for the low helminth species richness observed in blue-spotted salamanders may be that none of the helminths recovered in this study was specific to salamanders. The component community was composed of generalists that infected other anurans, or gastropods hosts, or both. Of the 3 helminth species recovered, only 1 adult nematode, *Cosmocercoides* sp., infected blue-spotted salamanders. A single juvenile *Cosmocercoides* sp. was located in the lungs of a single salamander and may represent *C. variabilis*, predominantly a parasite of toads and tree frogs (Vanderburgh and Anderson, 1987) and may be acquired by these salamanders from toad populations at this location. Blue-spotted salamanders commonly feed on terrestrial molluscs in Wisconsin and, therefore, the possibility also exists that *Cosmocercoides dukae*, a parasite of terrestrial molluscs that survives in amphibians that feed on molluscs, may also be present (Vanderburgh and Anderson, 1987; Bolek, 1997). Of the 25 *Cosmocercoides* sp. nematodes recovered, 9 were adults, with 3 males and 6 females; none was gravid.

Unfortunately, few studies have examined helminth community structure of salamanders and anurans from the same location. Yoder (1998) examined 3 species of anurans (*B. a. americanus*, *Pseudacris crucifer*, and *Rana sylvatica*) and 3 species of caudate amphibians (*A. laterale*, *Ambystoma tigrinum*, and *Notophthalmus viridescens*) from southeastern Wisconsin. He indicated that all 3 anurans were parasitized by nematodes belonging to the same 3 genera (*Cosmocercoides*, *Oswaldocruzia*, and *Rhabdias*) and served as intermediate hosts to the same group of larval platyhelminths (*Fibricola texensis*, *Mesocestoides* sp., and unidentified metacercariae). More importantly, in his study caudate amphibian component communities were species-poor compared with the anuran hosts he examined. All 3 caudatans were parasitized by *Cosmocercoides* sp., whereas *A. laterale* and *A. tigrinum* were infected with *Phyllodistomum americanum*, a trematode specific to *Ambystoma* salamanders (Tiekotter and Coggins, 1982). In another study, Muzzall (1991b) examined helminth infracommunities of eastern newts, *N. viridescens*, from Turkey Marsh, Michigan, a location from which Muzzall (1991a) also examined bullfrogs, *R. catesbeiana*, and green frogs for helminth infracommunities 2 yr ago. His data indicate that the only gravid helminths (*Bothriocephalus rarus* and *Telorchis corti*) infecting newts at this location were specific to salamanders or snakes and turtles but not anurans, whereas other helminth species (*Halipegus* sp. *Megalodiscus temperatus*, *Falcaustra catesbeianae*), which reached maturity and infected frogs from this location 2 yr ago, had a very low prevalence (1%) and intensity (1) and were not gravid in newts. Results from Muzzall's (1991a, 1991b) work and our study suggest that anuran helminths may not colonize and reach maturity in caudatans commonly. This may contribute to the depauperate helminth communities observed in salamanders in this study.

Size of hosts also appeared to be important in structuring helminth communities in anurans, with abundance and species richness being higher in adult than in metamorph frogs and toads. Adult leopard frogs and adult American toads were similar in size and had similar species richness, whereas metamorph leopard frogs and metamorph toads had less diverse communities dominated by larval trematodes. This indicates that larval trematodes were the first members of the helminth community to become established in this amphibian assemblage. The 2 adult anuran species showed no difference in overall prevalence and mean species richness, whereas adult toads had significantly higher helminth mean abundance. The differences in abundance observed in toads and leopard frogs may be caused by the presence of *R. americanus*, the most abundant direct–life cycle nematode recovered, which was restricted to toads (Baker, 1987). Adult anurans had a bigger gape size, larger surface area, and longer time to acquire helminth communities than metamorph individuals. Because larval platyhelminths could not be counted accurately and may be acquired throughout the tadpole and postmetamorph stages of the amphibians examined, they were excluded from abundance analysis.

Unlike toads and leopard frogs, metamorph and adult salamanders had similar species richness. This was because of metamorphs being heavily infected with echinostomatid metacercariae and adults harboring 3 species with low prevalence and mean intensity. It is unclear why adult salamanders had a lower prevalence and mean intensity of echinostomatid metacercariae compared with metamorphs. Martin and Conn (1990) studied the pathogenicity and cyst structure of echinostomatid metacercariae infecting the kidneys of green frogs and northern leopard frogs. As in our study, they found metacercariae cysts occurring in the ventrolateral renal cortex of the kidneys of frogs, with some metacercariae being confined to the lumen of the Bowman's capsules. They indicated that some metacercariae in frogs were dark brown and contained worms that were in various stages of decomposition. These results indicate that at least in frogs some infections by larval forms may be lost over time, and this may be an explanation of why adult blue-spotted salamanders had a lower prevalence and mean intensity of echinostomatid metacercariae than metamorph individuals. More importantly, our data indicate that, unlike adult anurans, older salamanders did not have richer helminth communities than metamorphs.

The low host specificity, helminth species richness, and low vagility of caudatans as compared with anurans suggest that local factors are important in structuring caudatan helminth communities of salamanders. This suggests that individual helminth species infecting salamanders may be more clumped in their geographic distribution as compared with anurans, and the role of other hosts may be important in structuring helminth communities of these hosts. When considering adult helminths that mature in amphibians, studies on blue-spotted salamanders from 4 locations in Wisconsin by Coggins and Sajdak (1982), Bolek (1997), Yoder (1998), this study and 2 locations from Michigan by Muzzall and Schinderle (1992) indicate that no adult helminth was recovered (*Cosmocercoides* sp., *C. dukae*, *P. americanum*, *Rhabdias ranae*, *Batracholandros magnavulvaris*, and *Brachycoelium salamandrae*) from infected salamanders at all these locations. More importantly, these were generalists that infected terrestrial snails, anurans, or other caudatans at these locations. Studies on helminth communities of American toads collected from 4 sites in Wisconsin by Coggins and Sajdak (1982), Yoder (1998), Bolek and Coggins (2000), and this study indicate that these hosts were dominated by direct–life cycle skin-penetrating nematodes common to bufonids (*R. americanus, C. variabilis*, and *O. pipiens*) at each site (Baker, 1987). Studies on green frogs collected from 3 sites in Wisconsin by Williams and Taft (1980), Bolek and Coggins (2001), and Yoder et al. (2001) and from 7 sites in Michigan by Muzzall (1991a) and Muzzall et al. (2001) were infected with 3 trematode species common to Ranid frogs at each site (*H. varioplexus*, *Halipegus eccentricus*, and *Glypthelmins quieta*) and 1 out of 2 sites from Canada by McAlpine (1997). Other studies on adult northern leopard frogs collected from 2 sites in Wisconsin by Williams and Taft (1980), this study, and 3 sites in Canada by McAlpine (1997) indicate that these frogs were also commonly infected with *Haematoloechus* spp., *Gorgoderina* spp., and *O. pipiens*, suggesting that helminth communities of anurans may be a lot more predictable than caudatans. We believe that because of their higher vagility, anuran populations may have a shorter distance to potential sources of infection and, therefore, their parasite populations may mix more often than caudatans. Results from our study and other studies on salamander helminthes suggest that salamander helminth communities may be dominated by generalists and their distribution correlated with ecological factors and overlapping habitats of other caudatan, anuran, and gastropod hosts and their parasites (Muzzall, 1991b; Bolek, 1997; Bolek and Coggins, 1998; Yoder, 1998; Mata-López et al., 2002).

ACKNOWLEDGMENTS

We thank Melissa Ewert and Luke Bolek for help in collecting frogs, toads, and salamanders. We also thank Augustin Jimenez Ruiz, Harold W. Manter Laboratory, University of Nebraska–Lincoln and an anonymous reviewer for improvements on an earlier draft of the manuscript.

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