Comp. Parasitol.
67(2), 2000 pp. 202–209

Seasonal Occurrence and Community Structure of Helminth Parasites from the Eastern American Toad, *Bufo americanus americanus*, 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 September 1996, 47 American toads, *Bufo americanus americanus* Holbrook, were collected from Waukesha County, Wisconsin, U.S.A., and examined for helminth parasites. Forty-six (98%) of 47 toads were infected with 1 or more helminth species. The component community consisted of 6 species, 3 direct-life-cycle nematodes, and 3 indirect-life-cycle helminths (2 trematodes and 1 metacestode). Totals of 2,423 individual nematodes (92%), 45 trematodes (2%), and 155 cestodes (6%) were found, with infracommunities being dominated by skin-penetrating nematodes. A significant correlation existed between wet weight and overall helminth abundance, excluding larval platyhelminths. Helminth populations and communities were seasonally variable but did not show significant differences during the year. However, a number of species showed seasonal variations in location in the host, and these variations were related to recruitment period.

KEY WORDS: *Bufo americanus*, American toad, *Cosmocercoides variabilis*, *Rhabdias americanus*, *Oswaldocruzia pipiens*, *Mesocestoides* sp., *Gorgoderina* sp., Trematoda, Nematoda, Cestoda, echinostome metacercariae, seasonal study, Wisconsin, U.S.A.

American toads, *Bufo americanus americanus* Holbrook, 1836, are large, thick-bodied terrestrial anurans found in North America near marshes, oak savannas, semiopen coniferous and deciduous forests, and agricultural areas. They range from Labrador and Hudson Bay to eastern Manitoba, south to eastern Oklahoma and the coastal plains, and are distributed throughout Wisconsin (Vogt, 1981). Toads are active foragers, differing from most anurans that are sit-and-wait predators (Seale, 1987). Although a number of surveys and natural history studies on the helminths and ecology of toads exists (Bouchard, 1951; Odlaug, 1954; Ulmer, 1970; Ulmer and James, 1976; Williams and Taft, 1980; Coggins and Sajdak, 1982; Joy and Bunten, 1997), no studies have used measures of helminth communities. Here we report on the helminth infracommunity and component community structure in American toads from southeastern Wisconsin.

Materials and Methods

American toads were collected from April to November of 1996 by driving 4.0-km sections of highways N and 67 (42°54′N, 88°29′W) in Eagle, Waukesha County, Wisconsin, U.S.A., during the night and collecting individuals as they crossed roads. 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 72 hr of capture. Snout-vent length (SVL) and wet weight (WW) were recorded for each individual. Toads were individually toe-clipped and frozen. At necropsy, the digestive tracts, limbs, body wall musculature, and internal organs were examined for helminth parasites. Each organ was individually placed in a Petri dish 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 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. Echinostome metacercariae were badly damaged during necropsy, and these were identified but not retained. Prevalence, mean intensity, and 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. Undigested stomach contents were identified to class or order following Borror et al. (1989). Stomach contents are reported as a percent = the number of arthropods in a given class or order, divided by the total number of arthropods recovered × 100. Voucher specimens have been deposited in the helminth collection of the H. W. Manter Laboratory (HWML), University of Nebraska State Museum, Lincoln, Nebraska, U.S.A. (accession numbers HWML

[1] Corresponding author. Current address: Department of Veterinary Pathobiology, Purdue University, West Lafayette, Indiana 47907, U.S.A. (e-mail: mgb@vet.purdue.edu).

Table 1. Prevalence, mean intensity, mean abundance, and total numbers of helminths found in 47 specimens of *Bufo americanus americanus*.

Species	Prevalence, No. (%)	Mean intensity ± 1 SD (range)	Mean abundance ± 1 SD	No. of worms recovered	Location
Trematoda					
Echinostome metacercariae*	3 (6.3)	13 ± 19 (1–35)	0.8 ± 5.1	39	Kidneys, body cavity
Gorgoderina sp.	1 (2.1)	6 ± 0 (6)	0.1 ± 0.9	6	Bladder
Cestoda					
Mesocestoides sp.*	6 (12.7)	25.8 ± 22 (12–70)	3.3 ± 11.3	155	Leg muscles
Nematoda					
Oswaldocruzia pipiens	41 (87)	8.5 ± 7 (1–31)	7.4 ± 7.1	349	Small intestine
Cosmocercoides variabilis	43 (91)	32.3 ± 31.5 (1–135)	29.6 ± 31.5	1,392	Lungs, body cavity, large and small intestine
Rhabdias americanus	43 (91)	15.8 ± 17.9 (1–75)	14.5 ± 17.7	682	Lungs, body cavity

* Underestimate.

15051, male *Oswaldocruzia pipiens*; 15052, male *Cosmocercoides variabilis*; 15053, *Rhabdias americanus*; 15054, *Gorgoderina* sp.; 15055, *Mesocestoides* sp.).

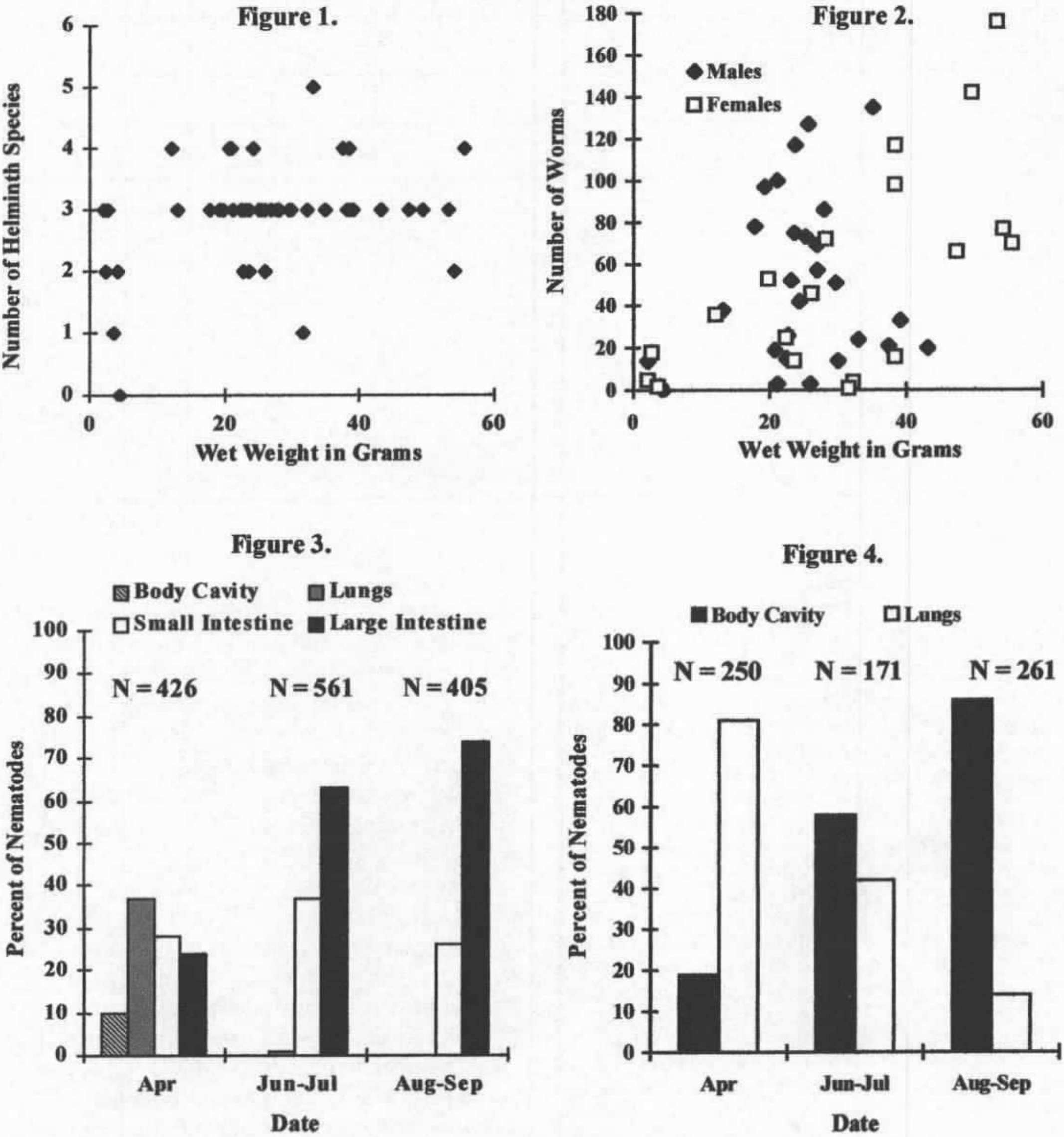
The chi-square test for independence was calculated to compare differences in prevalence among host sex, seasonal differences in prevalence, and seasonal differences in location of nematodes in the host. Yates' adjustment for continuity was used when sample sizes were low, and a single-factor, independent-measures analysis of variance was used to compare among seasonal differences in mean intensity and mean helminth species richness (Sokal and Rohlf, 1981). 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 amphibian. Because WW gave a stronger correlation than SVL in each case, it is the only parameter reported. Because of low sample sizes during certain collection periods, data were pooled on a bimonthly basis to form samples of 15 to 16 toads per season. Larval platyhelminths were not included in the seasonal analysis, because they can accumulate throughout an amphibian's life.

Results

A total of 47 American toads, 28 males and 19 females, was collected. The overall mean SVL and WW of toads was 56.6 ± 12.5 mm (range = 26.2–72.6 mm) and 26.6 ± 13.5 g (range = 2.19–55.5 g), respectively. No significant difference existed in numbers of male toads and female toads collected throughout the year ($\chi^2 = 1.72$, $P > 0.05$). Although female toads were larger (58.2 ± 15.4 mm) and heavier (30.5 ± 17.3 g) than males (55.5 ± 10.2 mm, 23.9 ± 9.7 g), these differences were not significant ($t = 0.73$, $P > 0.05$, $t'_s = 1.50$, $P > 0.05$). Stomach contents analyses revealed that the toads fed mostly on ants (98%), with beetles and other terrestrial arthropods representing a small portion of the diet (2%).

Forty-six (98%) of 47 toads were infected with 1 or more species of helminths. The component community consisted of 6 species, 3 direct-life-cycle nematodes, and 3 indirect-life-cycle helminths (2 trematodes and 1 metacestode). Overall mean helminth abundance, excluding larval platyhelminths, was 55.7 ± 45.3 worms per toad infracommunity (range = 0–180). Prevalence was highest for nematodes, ranging from 91% for *Cosmocercoides variabilis* Harwood, 1930, and *Rhabdias americanus* Baker, 1978, to 87% for *Oswaldocruzia pipiens* Walton, 1929. Prevalence for indirect life cycle parasites was generally low, being highest for the cestode *Mesocestoides* sp. (12.7%) and lowest for *Gorgoderina* sp. (2.1%) (Table 1). No significant differences existed in prevalence between male and female toads for any of the 6 helminth species recovered. Mean intensity differed significantly only in *Mesocestoides* sp., being higher in male (32.7 ± 32) than in female toads (19 ± 4.6, $t'_s = 4.70$, $P < 0.05$).

Mean helminth species richness was 2.9 ± 0.9



Figures 1–4. **1. Wet weight versus number of helminth species per individual of the American toad, *Bufo americanus americanus*, $r = 0.31$, $P < 0.05$. 2. Wet weight versus total helminth abundance, excluding larval platyhelminths, in American toads, *B. a. americanus*, overall $r = 0.47$, $P < 0.01$; female toads $r = 0.57$, $P < 0.01$; and male toads $r = 0.20$, $P > 0.05$. 3. Seasonal distribution of the relative proportions of *Cosmocercoides variabilis* recovered in the body cavity, lungs, small intestine, and large intestine of *B. a. americanus*. *N* equals number of nematodes recovered in each sampling period. 4. Seasonal distribution of the relative proportions of *Rhabdias americanus* recovered in the body cavity and lungs of *B. a. americanus*. *N* equals number of nematodes recovered in each sampling period.**

species per toad. Infections with multiple species were common, with 0, 1, 2, 3, 4, and 5 species occurring in 1, 2, 6, 30, 7, and 1 host, respectively. No statistically significant differences in mean helminth species richness were found between male (3.0 ± 0.86) and female toads (2.8 ± 0.85, $t = 0.83$, $P > 0.05$). There was a significant positive correlation between WW and helminth species richness per toad ($r = 0.31$, $P < 0.05$, Fig. 1). However, this relationship became insignificant when a single uninfected toad was removed ($r = 0.20$, $P > 0.05$). A significant

Table 2. Seasonal prevalence and mean intensity of 3 species of nematodes in *Bufo americanus americanus*.

Species		Apr	Jun–Jul	Aug–Sep	Statistic	P
Cosmocercoides variabilis	Prevalence	93% (14/15)	88% (14/16)	94% (15/16)	$\chi^2 = 0.5$	$P > 0.05$
	Mean intensity ± 1 SD	30.4 ± 28.5	40 ± 31.7	27 ± 34.6	F = 0.65	$P > 0.05$
Oswaldocruzia pipiens	Prevalence	93% (14/15)	88% (14/16)	81% (13/16)	$\chi^2 = 1.1$	$P > 0.05$
	Mean intensity ± 1 SD	7 ± 6.7	10 ± 8.1	8.3 ± 6.1	F = 0.63	$P > 0.05$
Rhabdias americanus	Prevalence	93% (14/15)	100% (16/16)	81% (13/16)	$\chi^2 = 3.7$	$P > 0.05$
	Mean intensity ± 1 SD	17.8 ± 21.6	10.7 ± 11.2	20 ± 19.8	F = 1.12	$P > 0.05$

positive correlation existed between WW and overall helminth abundance, excluding larval platyhelminths ($r = 0.47$, $P < 0.01$, Fig. 2), although this correlation was only significant for female toads ($r = 0.57$, $P < 0.01$) and not for males ($r = 0.20$, $P > 0.05$). Similar results were obtained for *C. variabilis* ($r = 0.41$, $P < 0.01$) and *O. pipiens* ($r = 0.43$, $P < 0.01$), whereas no significant correlation was observed for *R. americanus* ($r = 0.27$, $P > 0.05$). When these analyses were performed separately for male and female hosts, significant positive correlations occurred only in female toads (*C. variabilis*, $r = 0.52$, $P < 0.05$; *O. pipiens*, $r = 0.58$, $P < 0.01$; *R. americanus*, $r = 0.54$, $P < 0.05$).

Only 1 male toad was infected with 6 *Gorgoderina* sp. during the early spring (April) collection. There was no significant seasonal difference in prevalence or mean intensity for any of the nematodes recovered (Table 2). Prevalence was highest during early spring for *O. pipiens* (93%), early summer (June–July) for *R. americanus* (100%), and late summer–early fall (August–September) for *C. variabilis* (94%). Mean intensities were higher during early summer for *C. variabilis* and *O. pipiens* and in late summer–early fall for *R. americanus*. Seasonally, there was a significant difference in location of *C. variabilis* ($\chi^2 = 556$, $P < 0.01$), and *R. americanus* ($\chi^2 = 232$, $P < 0.01$). *Cosmocercoides variabilis* occurred in greater numbers in the body cavity and lungs during the early spring and in the small and large intestines during early summer and late summer–early fall collections (Fig. 3). Individuals of *Rhabdias americanus* were found primarily in the lungs during early spring and progressively increased in numbers in the body cavity during early summer and late summer–early fall collections (Fig. 4). The nematode *O. pipiens* showed no seasonal variation in location and was found in the small intestine throughout the year. *Oswaldocruzia pipiens* was significantly correlated with *C. variabilis* ($r = 0.54$, $P < 0.01$) in both male ($r = 0.51$, $P < 0.01$) and female toads ($r = 0.58$, $P < 0.01$) (Fig. 5) but was not significantly correlated with *R. americanus* ($r = 0.23$, $P > 0.05$) in either male ($r = 0.23$, $P > 0.05$) or female toads ($r = 0.24$, $P > 0.05$).

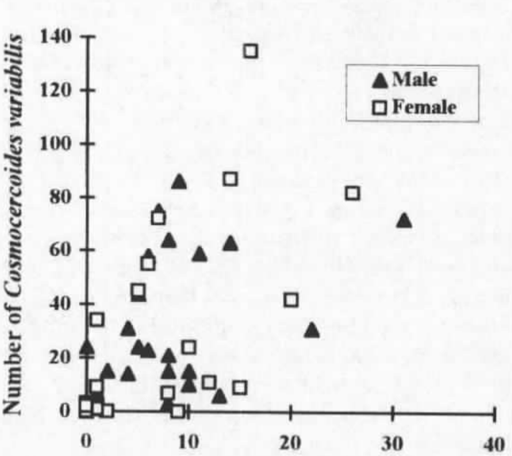


Figure 5. Number of *Oswaldocruzia pipiens* versus *Cosmocercoides variabilis* in *Bufo americanus americanus*, overall $r = 0.54$, $P < 0.01$; female toads $r = 0.58$, $P < 0.01$; and male toads $r = 0.51$, $P < 0.01$.

Mean species richness varied throughout the year, being highest (3.26 ± 0.79) in early spring, intermediate (2.88 ± 0.71) in early summer, and lowest during the late summer–early fall collection (2.62 ± 0.95), although these differences were not statistically significant (F = 2.3, $P > 0.05$). Wet weight of toads showed similar seasonal variability, but these differences were also not significant (F = 2.99, $P > 0.05$).

Discussion

The component community of Wisconsin toads was similar to those of other published reports (Bouchard, 1951; Odlaug, 1954; Ulmer, 1970; Ulmer and James, 1976; Williams and Taft, 1980; Coggins and Sajdak, 1982; Joy and Bunten, 1997; Yoder, 1998). Toad helminth infracommunities were dominated by 3 species of skin-penetrating nematodes with high overall prevalence and mean intensities and with few toads infected by indirect-life-cycle parasites.

Bladder flukes of the genus *Gorgoderina* are common parasites of amphibians, but few life-cycle studies exist (Prudhoe and Bray, 1982). The life cycles of *Gorgoderina attenuata* Stafford, 1902, and *Gorgoderina vitelliloba* Olsson, 1876, have been determined. For these species, amphibians acquire infection by feeding on semiaquatic insect larvae or tadpoles, and the worms excyst in the stomach and migrate to the kidneys and bladder (Rankin, 1939; Smyth and Smyth, 1980). The low prevalence (2.1%) and intensity (6) of *Gorgoderina* sp. observed in our study were not surprising, since analyses of stomach contents revealed few kinds of arthropods. This is characteristic of actively foraging species such as toads. Ants made up the largest portion of the diet, with beetles and other terrestrial arthropods being found less frequently. Kirkland (1904) also found that ants and beetles made up the greatest portion of the diet of 149 toads from New England, U.S.A. These results are similar to other investigations on diet of species of *Bufo* (Toft, 1981; Collins, 1993; Indraneil and Martin, 1998), where ants and beetles appeared to be an important food item in the diet of toads. Toft (1981) reported that ants made up 64% to 91% of the arthropods consumed by 3 South American toad species, while Collins (1993) mentioned that ants and beetles were important items in the diet of 5 species of *Bufo* from Kansas, U.S.A. Because most trematodes of amphibians use aquatic or semiaquatic arthropods as intermediate hosts (Prudhoe and Bray, 1982), these observations may indicate why toads usually have low species richness and prevalence of adult trematodes (Williams and Taft, 1980; Coggins and Sajdak, 1982; McAllister et al., 1989; Goldberg and Bursey, 1991a, 1991b, 1996; Goldberg et al., 1995; Bursey and Goldberg, 1998).

The most commonly occurring nematode was *C. variabilis,* with a total of 1,392 worms recovered. Vanderburgh and Anderson (1987) studied the seasonal transmission of this species in American toads from Ontario, Canada. They observed J_4 larvae in the lungs during the breeding season and adult worms in the rectum of toads throughout the year. They suggested that toads may acquire *C. variabilis* soon after emerging in the spring and that transmission may decline during summer and fall. However, they stated that this may have been an artifact of sampling, because all toads collected after the breeding season were from another location and may have had a lower prevalence and mean intensity of *C. variabilis.* Vanderburgh and Anderson (1987) also observed larvae in the lungs of 5 toads collected in October of the following year and concluded that transmission probably occurs throughout the year.

Data from the present study suggest that the breeding period may be important in transmission of *C. variabilis* in adult toads. All our toads were collected from the same general location and had high prevalence and mean intensities throughout the year. Although the differences were not significant, mean intensity increased after the breeding season and decreased during the late summer–early fall collection. Ten percent of the worms recovered during April were located in the body cavity, 37% were located in the lungs, and 28% and 24% were located in the small and large intestine, respectively. Subsequent sampling revealed that only 1 toad collected during June had 6 larvae in the lungs, with all other worms being recovered from the small and large intestine. Baker's (1978a) study on the life cycle of *Cosmocercoides dukae* Holl, 1928 (=*C. variabilis*) in toads revealed that 8–10 days are required for larvae to reach the lungs, and more than 30 days at 14–18°C to migrate to the rectum and develop to a gravid stage. Our observations suggest that toads became infected during the breeding season, and there appeared to be a decline during summer and early fall. Unfortunately, no toads were collected during October, and therefore it is not known if infection may occur during the fall (but see below). All adult female worms recovered throughout the year were gravid, indicating that eggs were being produced from April through September.

The second most frequently recovered nematode was *R. americanus,* primarily a parasite of toads (Baker, 1979a, 1987). Few studies exist on the seasonal occurrence of species of *Rhabdias* in amphibians (Lees, 1962; Plasota, 1969; Baker, 1979b). Lees (1962) studied the seasonal occurrence of *Rhabdias bufonis* Schrank, 1788, in its host, *Rana temporaria* Linnaeus, 1758, in England, and Baker (1979b) studied the seasonal occurrence of *Rhabdias ranae* Walton, 1929, in the wood frog, *Rana sylvatica* Le Conte, 1825, in Canada. Prevalence and intensities in these species were lowest during summer and highest in spring and early fall. Baker (1979b) observed many subadult worms in the body cavity of wood frogs during late summer and early fall, with no worms being found in the body cavity during early spring and few worms in the fall. Worms occurred in the lungs during early spring and fall, while few were found in the lungs during late summer and early fall. Baker (1979b) concluded that transmission of *R. ranae* occurs throughout the summer and early fall, with worms maturing in the lungs during the fall and overwintering in their hosts.

During this study, no significant differences in prevalence or mean intensity were observed throughout the collection period, although the location (lungs or body cavity) of worms varied during the year. Most *R. americanus* recovered in April occurred in the lungs, with numbers of worms in the lungs decreasing during early summer (June–July) and late summer–early fall (August–September). In contrast, the number of worms in the body cavity increased during the June–July and August–September collections. Therefore, transmission of this species occurred during the summer and early fall, with worms overwintering in their host. These results are consistent with earlier studies of seasonal distribution of other species of *Rhabdias* (Lees, 1962; Baker, 1979b).

Oswaldocruzia pipiens also had high prevalence but lower mean intensities than the other 2 species of nematodes recovered. Because of its fast migration, reaching the stomach and small intestine within 1 to 3 days of infection (Baker, 1978b), differences in location of these worms within the host were not observed. Prevalence and mean intensity were variable but not significant over the course of this study. Baker (1978b), in a seasonal study of *O. pipiens* in wood frogs, observed peak prevalence and intensity during spring (May–June) and early fall (September–October) in Ontario, Canada. He stated that worms overwintered in the host and that transmission occurred in early spring, with an initial decline during early summer and continued transmission during summer and early fall. A significant positive correlation existed for this species and *C. variabilis* but not for *R. americanus,* which suggested that toads became infected with *O. pipiens* and *C. variabilis* during the same time and in the same places, while infection with *R. americanus* occurred at a later time during the summer. Hosts that contain different species of adult parasites that co-occur in an infracommunity may contaminate an area when they release eggs in their hosts' feces. Therefore, acquisition of a certain parasite species by a host may often be coupled with the acquisition of other species into the infracommunity. The spring breeding period may also be important in the recruitment of *O. pipiens* in toads at our study site. Because toads were not collected during October, it is not known if recruitment occurs during this time. If infection occurs during the fall, as Baker's (1978b) data for wood frogs imply, *C. variabilis* may also be acquired in the fall.

Significant, positive relationships between WW and species richness and abundance were observed in toad helminth communities. However, significant relationships between WW and abundance were observed only in female toads. Interestingly, the largest toads collected were females, and these had the highest intensities of helminths; therefore, they may provide a greater surface area for colonization by skin-penetrating nematodes. Similar observations were reported by McAlpine (1997) for female leopard frogs, which were significantly larger than males. Although species richness also showed a significant positive relationship with WW, once the single noninfected individual was excluded from the calculation, the relation became nonsignificant. Therefore, no conclusions can be drawn from this relationship. Seasonal variance in species richness was not significant in *B. a. americanus,* with toad infracommunities being dominated by 3 skin-penetrating nematodes throughout the year. The toad's terrestrial habitat and diet of ants and beetles may be important in excluding transmission of adult and larval trematodes, unlike other anurans such as semiaquatic species of *Rana,* which spend more time in an aquatic environment and have a broader diet of semiaquatic invertebrates (Muzzall, 1991; McAlpine, 1997; Bolek, 1998).

Acknowledgments

We thank Melissa Ewert and Luke Bolek for help in collecting toads. We also thank 2 anonymous reviewers and the editors, Drs. W. A. Reid and J. W. Reid, for improvements on an earlier draft of the manuscript.

Literature Cited

Baker, M. R. 1978a. Transmission of *Cosmocercoides dukae* (Nematoda: Cosmocercoidea) to amphibians. Journal of Parasitology 64:765–766.

———. 1978b. Development and transmission of *Oswaldocruzia pipiens* Walton, 1929 (Nematoda: Trichostrongylidae) in amphibians. Canadian Journal of Zoology 56:1026–1031.

———. 1979a. The-free living and parasitic development of *Rhabdias* spp. (Nematoda: Rhabdiasidae) in amphibians. Canadian Journal of Zoology 57: 161–178.

———. 1979b. Seasonal population changes in *Rhabdias ranae* Walton, 1929 (Nematoda: Rhabdiasidae) in *Rana sylvatica* of Ontario. Canadian Journal of Zoology 57:179–183.

———. 1987. Synopsis of the Nematoda Parasitic in Amphibians and Reptiles. Occasional Papers in Biology, Memorial University of Newfoundland, St. John's, Newfoundland, Canada. 325 pp.

Bolek, M. G. 1998. A seasonal and comparative study of helminth parasites in nine Wisconsin amphibians. M.S. Thesis, University of Wisconsin–Milwaukee. 134 pp.

Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An Introduction to the Study of Insects, 6th ed. Harcourt Brace College Publishers, Philadelphia, Pennsylvania. 875 pp.

Bouchard, J. L. 1951. The platyhelminths parasitizing some northern Maine Amphibia. Transactions of the American Microscopical Society 70:245–250.

Bursey, C. R., and S. R. Goldberg. 1998. Helminths of the Canadian toad, *Bufo hemiophrys* (Amphibia: Anura), from Alberta, Canada. Journal of Parasitology 84:617–618.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. Journal of Parasitology 83:575–583.

Coggins, J. R., and R. A. Sajdak. 1982. A survey of helminth parasites in the salamanders and certain anurans from Wisconsin. Proceedings of the Helminthological Society of Washington 49:99–102.

Collins, J. T. 1993. Amphibians and Reptiles in Kansas, 3rd ed. The University of Kansas Museum of Natural History, Lawrence, Kansas, Public Education Series 13. 397 pp.

Goldberg, S. R., and C. R. Bursey. 1991a. Helminths of the red-spotted toad, *Bufo punctatus* (Anura: Bufonidae), from southern Arizona. Journal of the Helminthological Society of Washington 58:261–269.

———**, and** ———. 1991b. Helminths of three toads, *Bufo alvarius, Bufo cognatus* (Bufonidae), and *Scaphiopus couchii* (Pelobatidae), from southern Arizona. Journal of the Helminthological Society of Washington 58:142–146.

———**, and** ———. 1996. Helminths of the oak toad (*Bufo quercicus,* Bufonidae) from Florida (U.S.A.). Alytes 14:122–126.

———**,** ———**, and I. Ramos.** 1995. The component parasite community of three sympatric toad species, *Bufo cognatus, Bufo debilis* (Bufonidae), and *Spea multiplicata* (Pelobatidae) from New Mexico. Journal of the Helminthological Society of Washington 62:57–61.

Indraneil, D., and G. N. Martin. 1998. *Bufo fergusonii.* Ecology. Herpetological Review 29:164.

Joy, J. E., and C. A. Bunten. 1997. *Cosmocercoides variabilis* (Nematoda: Cosmocercoidea) populations in the eastern American toad, *Bufo a. americanus* (Salienta: Bufonidae), from western West Virginia. Journal of the Helminthological Society of Washington 64:102–105.

Kirkland, A. H. 1904. Usefulness of the American toad. Farm Bulletin, U.S. Department of Agriculture, Washington, D.C., 196:1–16.

Lees, E. 1962. The incidence of helminth parasites in a particular frog population. Parasitology 52:95–102.

McAllister, C. T., S. J. Upton, and D. B. Conn. 1989. A comparative study of endoparasites in three species of sympatric *Bufo* (Anura: Bufonidae), from Texas. Proceedings of the Helminthological Society of Washington 56:162–167.

McAlpine, D. F. 1997. Helminth communities in bullfrogs (*Rana catesbeiana*), green frogs (*Rana clamitans*), and leopard frogs (*Rana pipiens*) from New Brunswick, Canada. Canadian Journal of Zoology 75:1883–1890.

Muzzall, P. M. 1991. Helminth infracommunities of the frogs *Rana catesbeiana* and *Rana clamitans* from Turkey Marsh, Michigan. Journal of Parasitology 77:366–371.

Odlaug, T. O. 1954. Parasites of some Ohio Amphibia. Ohio Journal of Science 54:126–128.

Plasota, K. 1969. The effect of some ecological factors on the parasitofauna of frogs. Acta Parasitologica Polonica 16:47–60.

Prudhoe, O. B. E., and R. A. Bray. 1982. Platyhelminth Parasites of the Amphibia. British Museum (Natural History)/Oxford University Press, London, England. 217 pp.

Rankin, J. S. 1939. The life cycle of the frog bladder fluke, *Gorgoderina attenuata* Stafford, 1902 (Trematoda: Gorgoderidae). American Midland Naturalist 21:476–488.

Seale, D. B. 1987. Amphibia. Pages 467–552 *in* T. J. Pandian and F. J. Vanberg, eds. Animal Energetics. Volume 2. Academic Press, San Diego, California.

Smyth, J. D., and M. M. Smyth. 1980. Frogs As Host-Parasite Systems. 1. Macmillan, London, England. 212 pp.

Sokal, R. R., and J. F. Rohlf. 1981. Biometry, 2nd ed. W. H. Freeman and Company, New York. 859 pp.

Toft, C. A. 1981. Feeding ecology of Panamanian litter Anurans: patterns in diet and foraging mode. Journal of Herpetology 15:139–144.

Ulmer, M. J. 1970. Studies on the helminth fauna of

Iowa I. Trematodes of amphibians. American Midland Naturalist 83:38–64.

———, **and H. A. James.** 1976. Studies on the helminth fauna of Iowa II. Cestodes of amphibians. Proceedings of the Helminthological Society of Washington 43:191–200.

Vanderburgh, D. J., and R. C. Anderson. 1987. Preliminary observations on seasonal changes in prevalence and intensity of *Cosmocercoides variabilis* (Nematoda: Cosmocercoidea) in *Bufo americanus* (Amphibia). Canadian Journal of Zoology 65:1666–1667.

Vogt, R. C. 1981. Natural History of Amphibians and Reptiles of Wisconsin. The Milwaukee Public Museum and Friends of the Museum, Inc., Milwaukee, Wisconsin. 205 pp.

Williams, D. D., and S. J. Taft. 1980. Helminths of anurans from NW Wisconsin. Proceedings of the Helminthological Society of Washington 47:278.

Yoder, H. R. 1998. Community ecology of helminth parasites infecting molluscan and amphibian hosts. Ph.D. Thesis, University of Wisconsin–Milwaukee. 138 pp.