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Source: *The Journal of Parasitology*, Vol. 82, No. 5 (Oct., 1996), pp. 702-706

Published by: The American Society of Parasitologists

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COMPARISON OF *LEPTORHYNCHOIDES THECATUS* (ACANTHOCEPHALA) RECRUITMENT INTO GREEN SUNFISH AND LARGEMOUTH BASS POPULATIONS

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ABSTRACT: The degree to which host suitability is a reflection of host community structure in generalist parasites was studied experimentally in the common fish acanthocephalan *Leptorhynchoides thecatus*. Previous study has shown that green sunfish (*Lepomis cyanellus*) are required, and largemouth bass (*Micropterus salmoides*) are suitable (but not required) hosts, where they occur sympatrically in natural communities. The present study examined populations of *L. cyanellus* and *M. salmoides* held separately in mesocosms and exposed to *L. thecatus* cystacanths via laboratory-infected *Hyaella azteca* (Amphipoda). Recruitment, maturation, and transmission of worms were examined over a 17-wk period and compared between fish species. Infections with *L. thecatus* were found as early as 2 wk after the introduction of cystacanth-infected amphipods, and by week 11 fishes of both species harbored gravid worms. Immature worms were observed in both host species by week 17 and were presumed to be a result of natural egg production and release resulting in infections of amphipods and the subsequent reinfection of fish. No significant difference in the prevalence, abundance, percentage of worms gravid, or time of parasite maturation was found between host populations. Results indicate that the different roles played by these host species in the maintenance of *L. thecatus* suprapopulations in natural systems are not due to intrinsic factors but rather to differences in host autecology and community structure.

Helminthologists long have recognized that not all species capable of hosting a parasite species play equivalent roles in maintaining the parasite's suprapopulation. The concept of host suitability in regard to generalist parasites was extended by Holmes (1979) who defined 3 categories: required, a species in which parasite recruitment, maturation, and egg production are sufficient to maintain the parasite suprapopulation in the absence of other host species; suitable, a species in which parasite recruitment, maturation, and egg production occur but at a level insufficient to maintain the parasite suprapopulation in the absence of a required host species; and unsuitable, a species in which the parasite occurs but does not mature and either contributes to the maintenance of the parasite suprapopulation by acting as a paratenic host or, conversely, results in loss from the system by acting as an ecological "sink." Our ability to generalize from these concepts is complicated by the fact that the degree of suitability is determined by both intrinsic (evolutionary) and extrinsic (ecological) factors, and further, because the relative influences of these factors may differ considerably among different host species.

The complexity of the interrelationships among members of a host community and the transmission dynamics of a parasite often make assignment of roles by use of experimental infections intractable. Holmes et al. (1977) developed a method for estimating the contribution of various host species to the maintenance of a parasite suprapopulation by estimating relative flow to and from each host species. Although useful for measuring the relative importance of host species, this method does not explicitly determine the category to which a host species belongs. Instead, determinations are made inferentially by comparison of relative flow. Esch et al. (1976) used a live-box technique to study recruitment of parasites, but this technique, in itself, does not allow assessment of the roles played by host populations of individual species within the community.

At Atkinson Reservoir (Holt County, Nebraska) Ashley and Nickol (1989) determined that all population parameters measured for the generalist fish acanthocephalan *Leptorhynchoides thecatus* varied considerably among the 4 piscine species constituting the community of definitive hosts. All estimates were highest in green sunfish (*Lepomis cyanellus*), and they were sequentially less in pumpkinseed sunfish (*Lepomis gibbosus*), largemouth bass (*Micropterus salmoides*), and bluegill sunfish (*Lepomis macrochirus*). In this sequence, the relative flow ratios (relative flow from ÷ relative flow to) were 1.17, 1.10, 0.76, and 0.25, respectively, suggesting that relative flow ratios of 1 or more, more than 0 but less than 1, and 0 might identify required, suitable, and unsuitable hosts, respectively. Based on these estimates, it was determined that *L. cyanellus* and *L. gibbosus* are required hosts and that *M. salmoides* and *L. macrochirus* are suitable hosts at Atkinson Reservoir.

Recognition of the categories defined by Holmes is necessary for assessing population dynamics of generalist parasites; however, categorical assignment of hosts based on standard infection parameters may have limited application beyond the site at which the estimates are made due to inherent complications. To examine the extent to which such categorizations are useful beyond the context of a particular study, transmission of *L. thecatus* was studied experimentally in separate populations of *L. cyanellus* and *M. salmoides*. These host species were utilized, in part, because of previous study on *L. thecatus* in laboratory-maintained green sunfish (Ewald and Nickol, 1989) and largemouth bass (Leadabrand and Nickol, 1993) that aid in distinguishing between possible intrinsic and extrinsic effects on the parasite's transmission.

MATERIALS AND METHODS

Twelve, 5,700-L cylindrical fiberglass mesocosms (2.1 m high by 1.8 m diameter) located on the grounds of Cedar Point Biological Station (University of Nebraska), Keith County, Nebraska, were used to conduct the study. Green sunfish were collected in Lancaster County, Nebraska, and largemouth bass were purchased from a fish hatchery in Red Willow County, Nebraska. *Hyaella azteca* and other aquatic invertebrates used for the maintenance of prey populations in the mesocosms were taken from Island Lake, Garden County, Nebraska, and amphipods used for laboratory infections were collected from Lancaster County. The me-

Received 24 January 1996; revised 25 April 1996; accepted 25 April 1996.

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socosms were filled with unfiltered water pumped from the Keystone Reservoir adjacent to the station grounds. These waters and the localities from which animals were collected are known (Samuel et al., 1976; Ewald and Nickol, 1989; Leadabrand and Nickol, 1993) to be free from the presence of *L. thecatus*. Thus, the introduction of acanthocephalans to the system was controlled by the investigators.

Five double-holed cinder blocks were placed at the bottom of each mesocosm to provide habitat and shelter for fish, and continuous aeration was achieved by pumping air through PVC pipes that forced water from the lower third of the water column to be recirculated to the surface. To each of 6 mesocosms, green sunfish were introduced, and to each of the remaining 6 mesocosms, largemouth bass were introduced. Host populations were limited to 10 fish to insure that subsequent parasite infection rates were not artificially high due to limited food resources. Largemouth bass were of small and medium size classes as defined by Werner et al. (1977); green sunfish ranged from medium to large (Table I). Fish size was randomized within populations. It was not possible to produce long-term, self-sustaining biotic communities within the mesocosms. Therefore, aquatic vegetation, amphipods, and other aquatic invertebrates were added at 3-wk intervals after initiation of the study to maintain a large community of prey items that included uninfected amphipods.

Eggs of *L. thecatus* obtained from centrarchid fishes collected from the Elkhorn River system in Antelope and Holt counties, Nebraska, were used to rear viable cystacanths in laboratory-maintained amphipods as detailed by Olson and Nickol (1995). Populations of amphipods exposed to *L. thecatus* eggs were pooled and sampled to estimate the prevalence and intensity of infections. Twelve amphipods were selected randomly from the pool and introduced to each mesocosm concurrently with the introduction of fish.

One mesocosm containing green sunfish and 1 mesocosm containing largemouth bass were drained 2 wk after the introduction of the fish and laboratory-infected amphipods to ascertain whether initial transmission of the parasite from the introduced amphipods had taken place; thereafter, 1 tank of fish of each species was drained at 3-wk census intervals. The mesocosms were established in the month of June and the final census was made in November. In duration and season, this time span corresponds roughly to the second annual peak of occurrence of *L. thecatus* in *L. cyanellus* and *M. salmoides* in Nebraska (Ashley and Nickol, 1989). Samples of the amphipod populations were collected on the 14th and 17th wk after the initiation of the study and examined for *L. thecatus* infections. Fish were killed immediately following the drainage of each mesocosm, and their intestines, pyloric ceca, mesenteries, and body cavities were examined for the presence of parasites. Recovered worms were prepared by standard procedures for examination by light microscopy.

Data were analyzed using a completely random design, with separate analyses of abundance, prevalence, mean intensity, and percentage of females gravid. Analyses were made both within (by week) and between host species for each population parameter estimated. For between-host species comparisons, data from weeks 5, 8, 11, 14, and 17 were pooled to examine overall differences. Because second generation worms were found only on 1 census interval, an *F*-test of these data could not be performed. Linear regression was used to examine overall effect of host size on the total number of worms recovered. Analyses of variance (ANOVA) were used to determine significant differences among means. Statistics were derived with SAS® using the General Linear Models procedure. Statistics for significant results of ANOVA are reported in the text parenthetically.

Ecological terms are used as recommended by Margolis et al. (1982), and relative flow was calculated as described by Holmes et al. (1977), with the modification used by Ashley and Nickol (1989).

RESULTS

Large numbers of amphipods regularly were found in the alimentary tracts of both green sunfish and largemouth bass upon dissection. Other invertebrates, such as aquatic beetles and chironomid larvae, also were found upon dissection, although in smaller proportions than amphipods.

Overall abundance of worms was 1.09 for green sunfish and

TABLE I. Overall numbers of introduced *Leptorhynchoides thecatus* recovered from 5 separate populations each of *Lepomis cyanellus* and *Micropterus salmoides* maintained in 10, 5,700-L mesocosms.*

Host species (n, range, mean ± SE)†	Category	Num- ber of worms	Inten- sity	Abundance ± SE
<i>Lepomis cyanellus</i>				
(34, 7.4–14.5, 11.2 ± 0.29)	Male	12	0–2	0.35 ± 0.10
	Female	25	0–4	0.73 ± 0.19
	Total	37	0–5	1.09 ± 0.25
<i>Micropterus salmoides</i>				
(48, 6.8–12.1, 8.28 ± 0.16)	Male	24	0–2	0.50 ± 0.11
	Female	21	0–4	0.44 ± 0.12
	Total	45	0–4	0.94 ± 0.16

* Individual mesocosms were maintained 5–17 wk postintroduction of *L. thecatus*. Data here are pooled by host species.

† Total number of fish examined; range of fish total lengths (cm); mean ± SE of fish total lengths (cm).

0.94 for largemouth bass (Table I). Abundance between census intervals ranged from 0.75 to 1.4 in green sunfish and 0.44 to 1.3 in largemouth bass. No significant difference was found in mean abundance of male or female worms between host species or between census intervals within each host species.

Overall, approximately half of the fish harbored *L. thecatus* (Table II). No significant difference in prevalence was found between host species. Green sunfish had a significantly higher overall mean intensity ($F = 7.24$; $df_{\text{host}} = 1$; $df_{\text{error}} = 8$; $P > F = 0.027$) with an average of 2.4 worms per infected fish compared to 1.9 in largemouth bass (Table II). A significant negative linear relationship between host size and total number of worms was found in largemouth bass ($F = 3.13$; $df_{\text{size}} = 1$; $df_{\text{error}} = 46$; $P > F = 0.084$). No such significant relationship was found in green sunfish.

Length of the prepatent period was not affected by host species. Numerous ovarian balls were seen in all female worms at the 2-wk preliminary examination. Initial egg production (fragmentation of ovarian balls) was seen first on week 11 in *L. cyanellus*, and from 1 worm in a largemouth bass on week 8. Fully embryonated eggs were observed in female worms recovered on weeks 14 and 17 in both host species. No significant difference was found between the percentage of females gravid (Table II). All male worms recovered were mature.

On week 17, 2 male worms of a second generation were recovered from green sunfish and in largemouth bass 3 male and 1 female worms of a second generation were obtained. Additionally, a male and female pair from a green sunfish were considered to be second generation, although their generational status was questionable.

DISCUSSION

Recruitment

The estimated abundance of cystacanths within the laboratory-infected amphipod pool was 1.2 (12 cystacanths recovered from a random sampling of 10 amphipods). This number is comparable to the mean abundance of recovered worms from the green sunfish and largemouth bass populations (1.09 and

TABLE II. Prevalence, mean intensity, percentage of females gravid, and percentage of second generation worms of introduced *Leptorhynchoides thecatus* recovered at 3-wk census intervals from 5 separate populations each of *Lepomis cyanellus* (LC) and *Micropterus salmoides* (MS) maintained in 10, 5,700-L mesocosms.

Week*	Prevalence (%)		Mean intensity		% Females gravid		% 2nd generation	
	LC	MS	LC	MS	LC	MS	LC	MS
5	57	33	2.00	2.00	0.0	0.0	0.0	0.0
8	60	60	2.33	2.17	0.0	12.5	0.0	0.0
11	25	22	3.00	2.00	80.0	0.0	0.0	0.0
14	43	73	2.67	1.75	100.0	80.0	0.0	0.0
17	57	56	2.24	1.6	80.0	60.0	55.5	50.0
Mean	48.4	48.8	2.45	1.90	52.0	30.5	†	†
SE	6.5	9.3	0.47	0.10	21.5	16.5		

* Number of weeks postintroduction of laboratory-infected amphipods (*Hyalella azteca*).

† Only 1 observation.

0.94, respectively) in which they were hosted by ~10 fish/host population (fish mortality resulted in the recovery of <10 individuals in some populations). This, albeit indirect, comparison of introduced vs. recovered worms suggests that high percentages of the introduced parasites were recruited into the fish populations.

Early in the course of infection of *L. thecatus*, the juvenile worms occur in the anterior third of the intestine and in pyloric ceca, but after 1 wk they are restricted entirely to the ceca (Uznanski and Nickol, 1982; Ewald and Nickol, 1989; Leadabrand and Nickol, 1993). All worms recovered in the preliminary 2-wk examination were obtained from ceca, indicating that recruitment took place before the second week. Early completion of recruitment is corroborated by the facts that the abundance of worms did not differ significantly between census intervals in either host species and that upon examination at each census interval an increase in the degree of maturation of first generation worms was observed.

Such successful recruitment is unlikely to have been due to a paucity of prey items available to the fish, as there was a large community of invertebrates found upon drainage in the mesocosms at each census interval. Recruitment might have been enhanced, however, by the relatively large size of the laboratory-infected amphipods (~7 mm in length) that were introduced. Cooper (1965) found that fish predation on amphipods is related to size of the prey, with larger amphipods preferred.

Transmission

Contamination with *Leptorhynchoides thecatus* from the repeated addition of invertebrate prey was controlled by introducing invertebrates from waters known to be free of the presence of this acanthocephalan, whose distribution in Nebraska is restricted entirely to the waterways of the Elkhorn River (Samuel et al., 1976). It was possible, however, that other parasites were introduced into the mesocosms that could, in theory, have affected the establishment and transmission of *L. thecatus*. Nevertheless, no parasite (other than individuals of *L. thecatus*) was found upon dissection of the fish.

It was not possible to make direct determinations of parasite generation and, thus, determinations were made on relative information and by inference. For example, no parasite recovered before week 14 was considered to be of second generation because the minimal time required for completion of a single

life cycle under laboratory conditions is approximately 12 wk (DeGiusti, 1949). Morphometric variability of fixed specimens prevented use of these data in making determinations, although observations of relative length before fixation provided a good indication of parasite maturity. Inferential data were useful for making determinations on male worms. For example, a large-mouth bass harbored a single gravid worm, indicating previous loss of male worms from this fish. This demonstrates that male *L. thecatus* may die as early as 14 wk. It would be expected, then, that the majority of male worms would be passed by 17 wk. The position of worms within the host's alimentary canal provided further evidence of generational status. Worms recovered from the intestinal tract constitute new infections as described above, i.e., they are ≤1-wk-old. The possibility of introduced amphipods surviving 14–17 wk after their introduction is minimal. Less than ¼ of amphipods survive 20 days postexposure to *L. thecatus* eggs in the laboratory (Uznanski and Nickol, 1980; Olson and Nickol, 1995). Thus, intestinal worms recovered on week 17 were considered to be second generation.

Second generation worms were recovered from both hosts species on week 17, indicating that release of eggs into the mesocosms began prior to week 14. Later release of eggs would not have allowed sufficient time for *L. thecatus* to develop to the infective stage in amphipods. It is likely that many of the amphipods that acquired infections in the mesocosms were consumed before the acanthellas had reached infectivity, which would account for the small number of second generation worms recovered at week 17. In nature, the greater volume of habitat into which eggs are dispersed must enhance the chance of survival to infectivity in amphipods.

Parenteral infections

Van Cleave (1920) and DeGiusti (1949) concluded that parenteral infections with *L. thecatus* are due to insufficient development in the intermediate host. Only 1 parenteral infection was found over the course of the study. If, in fact, many second generation worms in amphipods were consumed by fishes before cystacanth infectivity was achieved, it is unlikely that occurrence of parenteral forms is explained by insufficient development in intermediate hosts. If it were, a greater number of parenteral worms would have been expected by week 17. The absence of parenteral worms is consistent with the hypothesis that such

forms result from infections of high intensities (Leadabrand and Nickol, 1993) as the size of the parasite infrapopulation did not exceed 15 cecal worms previously found to be about the maximum intensity in these host species (Uznanski and Nickol, 1982; Ewald and Nickol, 1989; Leadabrand and Nickol, 1993).

Host suitability

Based on the relative flow data of Ashley and Nickol (1989), green sunfish were predicted to be required hosts and largemouth bass suitable hosts for *L. thecatus*. This premise suggests that largemouth bass alone would not support the parasite suprapopulation from generation to generation, whereas this would be expected in the green sunfish populations. Except for mean intensity, population parameters measured in this study (total number of male and female worms, prevalence, percentage of females gravid, and percentage of second generation worms) did not differ significantly between host species. The mean intensity measured for green sunfish might be artificially high due to higher host mortality (Table I). Because no significant difference between species was seen in the abundance of worms, the fact that they were hosted by fewer fish in the green sunfish populations could account for the difference. Data obtained from this study lead to the conclusion that green sunfish and largemouth bass, when held in single populations, are equally capable of sustaining a suprapopulation of *L. thecatus*.

Host suitability is affected by the rate at which a parasite matures, e.g., hosts in which parasites mature quickly make a greater contribution to the parasite suprapopulation over time than do those in which maturation is slow. However, the maturation rate of *L. thecatus* did not differ between host species, and thus, this intrinsic aspect of host suitability is an unlikely explanation for the differences in suitability observed in nature. This is further corroborated by laboratory data (Ewald and Nickol, 1989; Leadabrand and Nickol, 1993).

Results of this study indicate that differences in host suitability exhibited by green sunfish and largemouth bass in nature are instead a result of ecological or extrinsic factors. For example, the mode of *L. thecatus* transmission is likely to differ between these fishes as a result of different habitats and prey items. Werner et al. (1977) studied habitat partitioning of centrarchids in 2 lakes in Michigan. They found that the niche of green sunfish was restricted to the shoreline at depths of less than 2 m where emergent vegetation was dense. Largemouth bass occupied deeper littoral zones and had almost no overlap with the habitat of green sunfish. These fishes were also found to segregate according to vegetation type; green sunfish were found among bullrushes, whereas largemouth bass were more abundant among the open water lilies. Young largemouth bass (<7.5 cm), however, utilized the shallow, medium, and deep regions of the littoral zone more equitably. Dietary differences between adult fish were also shown by Werner (1977). Green sunfish preferred small- to medium-sized invertebrate prey, whereas largemouth bass usually were piscivorous, although their diet was supplemented with macroinvertebrates. The significant inverse relationship found between host size and number of worms in largemouth bass is likely a reflection of these facts. Bluegill sunfish were shown to shift from shallow to deeper littoral zones in the presence of more aggressive and habitat-restricted green sunfish (Werner and Hall, 1977). Of the sun-

fishes, green sunfish are considered most resistant to competitive interactions, and they have been shown to protect their resources by both aggressive behavior and highly efficient foraging of prey (Moyle and Cech, 1988).

Because amphipods feed on the dense aquatic vegetation near the shores of lakes (Cooper, 1965), fishes that utilize this habitat would be expected to have the highest prevalence of *L. thecatus* infections. Green sunfish, due to their feeding and habitat preferences, probably acquire the majority of their infections directly from predation on amphipods. In contrast, largemouth bass might obtain the majority of their infections by postcyclic transmission or by predation on paratenic hosts, including bass fry, which spend more time in the shallow littoral zone than do adult bass. It is not possible to determine the origin of infection upon examination, and it is, therefore, difficult to determine the effects different modes of transmission have on infection parameters in natural systems.

Community structure effects on host suitability

From sites other than Atkinson Reservoir, studies that assess the suprapopulation dynamics of *L. thecatus* indicate that basses are the principal hosts (Van Cleave, 1919, 1923; Van Cleave and Mueller, 1934). However, green sunfish were absent from those communities, and basses were the predominate centrarchid fishes. At Atkinson Reservoir, members of the genus *Lepomis* are the most abundant centrarchid species, whereas the only bass present, *M. salmoides*, occurs less frequently. Relative flow estimates in Cold Lake, Alberta, Canada, led Holmes (1979) to conclude that whitefish (*Coregonus clupeaformis*) was the required definitive host of the acanthocephalan *Echinorhynchus salmonis*. However, studies of *E. salmonis* at other localities have found quite different patterns of flow that reflect differences in the structure of the host communities (Kennedy, 1985). Amin (1987) found similar host role changes among differing populations of the acanthocephalan *Pomphorhynchus bulbocolli*, although explicit use of relative flow estimates to determine host roles was not employed.

The present study demonstrates the effects of alleviating host community structural influences on host suitability in a generalist parasite. Results show that inferences made possible by the categorization of host suitability are dependent, in part, upon a high degree of ecological similarity among geographic sites.

ACKNOWLEDGMENTS

We thank especially Dennis Richardson, for help in the collection and preparation of materials, and Richard Clopton for assistance collecting sunfish. Ronald Randall provided considerable help with the maintenance of the mesocosms. Ken Volle provided access to his property and assisted in the collection of fish. William Barrens of the Crescent Lake National Wildlife Refuge gave permission to collect invertebrates from restricted waters. This work was supported, in part, by an Aston C. Cuckler Fellowship.

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