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A MARK–RECAPTURE STUDY OF TREMATODE PARASITISM IN OVERWINTERED *HELISOMA ANCEPS* (PULMONATA), WITH SPECIAL REFERENCE TO *HALIPEGUS OCCIDUALIS* (HEMIURIDAE)

Timothy M. Goater, Allen W. Shostak*, Julie A. Williams, and Gerald W. Esch
Department of Biology, Wake Forest University, Box 7325 Reynolda Station,
Winston-Salem, North Carolina 27109

ABSTRACT: A collection of 556 snails, *Helisoma anceps,* was made from a pond in the Piedmont area of North Carolina during October 1987. Snails were measured and assayed for trematode parasitism, and then 500 randomly selected individuals were marked and returned to the pond. Collections made between 23 March and 12 July 1988 resulted in recapture of 86 marked snails. Five trematode species were present in the fall collection, dominated by the hemiurid *Halipegus occidualis* (present in 31.5% of all snails, and 84.5% of infected snails). Antagonistic interactions between *H. occidualis* and other trematodes were indicated by a lower proportion of multiple-species infections in the fall collection than predicted from trematode prevalences and snail size distribution. Spring collections resulted in recapture of 31 snails that had patent infections in the fall collection. Of these, 7 of 27 previously infected with *H. occidualis* no longer harbored patent infections, nor did 2 of 3 previously infected with *Megalodiscus temperatus,* or the single recaptured snail that previously had a patent infection with *Diplostomulum scheuringi.* Necropsy of 5 of 7 snails previously infected with *H. occidualis* revealed an intact ovotestis and no parasites, confirming loss of infection and reversal of parasitic castration. The number of new patent infections increased markedly between late March and early June, suggesting that acquisition of new infections commenced soon after snails emerged from the substratum in early March. Snail survival over the winter was independent of parasitic infection. Growth rates of snails harboring *H. occidualis* before and after the winter were similar to uninfected snails, but snails that became patent subsequent to the fall collection grew less than predicted. The consistency observed for fall and spring prevalences of *H. occidualis* reflects a dynamic balance among processes that tend to increase prevalence and others that tend to decrease it.

The dynamics and coevolutionary implications of snail–trematode interactions have received a great deal of attention in recent years (e.g., Minchella et al., 1985; Brown et al., 1989; Kuris, 1989; Sousa, 1989). Larval trematodes may reduce snail growth significantly (Baudoin, 1975; Sousa, 1983), reduce reproduction (Kuris, 1974; Crews and Esch, 1986), and alter behavior (Curtis, 1985). Most of these observations, however, involved comparisons of infected versus uninfected snails without benefit of a time course investigation that would permit following infections in individual snails. Few have adopted the approach of Sousa (1983) to monitor snail–trematode dynamics through time by mark–release–recapture protocols. Snail–trematode systems are particularly amenable to mark–recapture studies because cercarial shedding provides a direct means of detecting patent infections without killing host individuals. Such an approach permits the assessment of the more dynamic aspects of host–parasite relationships.

Monitoring individuals in a host population over time makes it possible to gain valuable information on parasite recruitment, snail size or age distributions, and the potential for intertrematode antagonism under field conditions. In this paper we examine these features, and others, in a pulmonate snail, *Helisoma anceps,* and its trematode fauna, focusing on the hemiurid, *Halipegus occidualis.*

Halipegus occidualis matures under the tongue in the mouth of green frogs, *Rana clamitans,* in a North Carolina farm pond (Charlie's Pond). Details of the life cycle have been described by Macy et al. (1960). The intramolluscan features are as follows: embryonated eggs of the parasite, each containing a spined miracidium, are swallowed by the frog and are voided with the feces. Miracidia hatch upon accidental ingestion by *H. anceps,* penetrate the gut wall, and migrate to the hepatopancreas where they transform into sporocysts. These, in turn, form rediae. Upon maturation, rediae devour the hepatopancreas and

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* Current address: Institut Maurice-Lamontagne, Fisheries and Oceans (Pêches et Océans), C.P. 1000, Mont-Joli, Québec, Canada G5H 3Z4.

then spill over into the ovotestis, rendering the snail castrated (Crews and Esch, 1986, 1987).

Crews and Esch (1986) reported that *H. occidualis* infected up to 55% of adult snails on a seasonal basis. This is a relatively high prevalence for trematode infection in a mollusc population (Anderson and May, 1979), particularly because 100% of the *H. anceps* with patent infections are castrated by the parasite. An important aspect of the population dynamics of *H. occidualis* is its ability to overwinter in snails, a conclusion based on similar prevalences in the fall and following spring (Crews and Esch, 1986). Castrated overwintered snails would be excluded from the usual period of intense egg laying by *H. anceps* that normally occurs in Charlie's Pond during May and June (Crews and Esch, 1986).

A population-level study, such as the one of Crews and Esch (1986), cannot, however, resolve critical aspects of snail–trematode interactions that may be involved during the overwintering period. For example, 2 hypotheses may be advanced to explain similarities in levels of parasite prevalence from fall and spring observations. First, it is possible that all infected snails retained their infections over the winter months. Alternatively, some snails might lose their infections, whereas others may acquire new infections during the winter. These hypotheses cannot be tested using the results from Crews and Esch (1986), as longitudinal studies on individual hosts are required.

The present study was undertaken to examine the dynamics of *H. anceps–H. occidualis* interactions over the winter months using individually marked snails. Fall patterns of trematode parasitism in a cohort of snails were characterized, and a mark–release–recapture method was used to follow the time course of infections.

MATERIALS AND METHODS

Fall collection

On 20 October 1987, snails were hand-collected from a U-shaped cove (10-m-wide inlet, 70-m shoreline) in Charlie's Pond. All snails encountered on the bottom substratum or emergent vegetation in the littoral zone were taken. The pond was described by Crews and Esch (1986). Snails were transported to the laboratory; they were marked by painting the shell with fast-drying yellow enamel paint and applying individual identification numbers with a fine-tipped indelible pen. Maximum shell diameter was measured with calipers to the nearest 0.05 mm. Snails were placed individually in 55-mm-diameter finger bowls containing pond water under ambient conditions (approx. 24 C; 14 L:10 D photocycle). After 2 days, each dish was examined for cercariae under 10–20× magnification. Due to the high prevalence of *H. occidualis*, external contamination of uninfected snails by cercariae of this species was possible. Infected *H. anceps* shed tens to thousands of cercariae of *H. occidualis* daily (Macy et al., 1960). If only a few (1–5) cercariae were present after 2 days, contamination was suspected and the water was replaced. If no cercaria was shed during the third 24-hr period, the snail was assumed to be uninfected. As a control group, 10% of the snails were selected at random, crushed, and examined for prepatent infections.

Release of snails and activity monitoring

On 26 October 1987 the remaining snails were randomly allocated to 5 groups and returned to the cove at 5 evenly spaced locations. Snails were scattered over a 2-m length of littoral zone in each location, within 1.5 m of shore.

Return visits were made at irregular intervals until 12 December 1987 to measure water temperatures (at 0.3 m depth) and to record sightings of marked snails. Visits to the pond recommenced on 1 March 1988. Starting on 23 March 1987, all marked snails that were observed were collected and returned to the laboratory.

Spring evaluation of marked snails

Marked snails were measured and checked for shedding of cercariae. Snails for which infection status was in doubt were dissected; otherwise, they were returned to the cove to their most recent site of collection.

Data analysis

Because most snails were recaptured only once, and the interval between recaptures for the remainder averaged 32 days, each recapture was treated as an independent observation for statistical analysis. Snail growth was assessed on the basis of living weight (W, mg), estimated from maximum shell diameter (D, mm) using the relationship: $\ln W = 2.89 \ln D - 1.72$ (Boerger, 1975). Data from uninfected snails were used to estimate the values a–d of the model:

$$W2 = \mathrm{a} + \mathrm{b}W1 + \mathrm{c}T + \mathrm{d}T^2,$$

where $W2$ is weight at recapture, $W1$ is initial weight, and T is days to recapture. A predicted $W2$ for each infected snail was calculated from its $W1$ and T, using this above model with values a–d estimated from uninfected snails. Observed and predicted $W2$s were compared using a sign test.

Other statistical treatments followed procedures in Sokal and Rohlf (1981). Data are reported as mean ± 1 SD unless otherwise indicated. Results were accepted as significant at $P < 0.05$.

RESULTS

Fall collection

A total of 556 snails was collected and marked. Shell diameters were 9.6 ± 1.1 mm (range: 6.6–13.7 mm). There were 349 (62.8%) snails that shed no cercaria. Patent infections (i.e., those in which cercariae were shed) were present in 207 (37.2%) snails and comprised 5 species: *H. occidualis* (31.5%), *Megalodiscus temperatus* (3.6%), *Diplostomulum scheuringi* (1.1%), 1 species with an ornatae-type cercaria, (0.7%), and 1 species with an armatae-type cercaria (0.4%). No multiple infection was observed.

Prevalence of *H. occidualis* increased with increasing snail size, whereas the remaining trematodes were most frequent in smaller hosts (Fig. 1). Nonshedding snails had a shell diameter of 9.5 ± 1.0 mm (n = 349). Shell diameters of shedding snails and their statistical comparison with diameters of nonshedding snails using Student's t-test were as follows: *H. occidualis,* 9.8 ± 1.0 mm, n = 175, $t = 3.02$, $P = 0.003$; *M. temperatus,* 9.5 ± 1.3 mm, n = 20, $t = 0.12$, $P = 0.905$; *D. scheuringi,* 8.5 ± 1.0 mm, n = 6, $t = 2.38$, $P = 0.018$; ornatae-type cercariae, 8.7 ± 1.7 mm, n = 4, $t = 1.63$, $P = 0.105$; armatae-type cercariae, 8.7 ± 0.3 mm, n = 2, not tested. Because 4 comparisons against the same group of uninfected snails were done, a Bonferroni adjustment (0.05/4 = 0.0125) was made to the chosen critical value of P. As a result, we conclude that only snails infected with *H. occidualis* had a shell size that differed significantly from nonshedding snails.

Multiple infections of *H. occidualis* with other trematodes were not observed, suggesting the possibility of antagonistic interactions. Confidence limits for an observation of 0% based on n = 556 are 0–0.54% (95% CL) and 0–0.83% (99% CL). If the presence of *H. occidualis* were independent of the presence of other trematodes, and also independent of snail size, then the expected frequency of multiple infections based on the product of separate probabilities is: 175/556 (*H. occidualis*) × 32/556 (other trematodes) = 1.81%, a value outside the upper 99% CL for the observed frequency. It may be that the presence of *H. occidualis* is independent of the presence of other trematodes, but that trematode infections are, for some other reason, related to snail size (as suggested by examination of Fig. 1). To test this, probabilities of co-occurrence were calculated independently for each snail size class (weighted by sample size) and then totaled. The result was that multiple infections should be expected in 0.99% of snails, still outside the upper 99% CL for the observed frequency. We concluded that *H. occidualis* co-occurred with other species of trematodes significantly less often than expected from their prevalences in the snail population.

Dissection of 56 snails as controls revealed that all 19 (33.9%) that were shedding cercariae of *H. occidualis* also harbored rediae (i.e., no false positives). However, there were some false negatives, as 4 of 37 nonshedding snails (10.8%) had prepatent infections with *H. occidualis.* Prepatent infections with other species were not found among the control group.

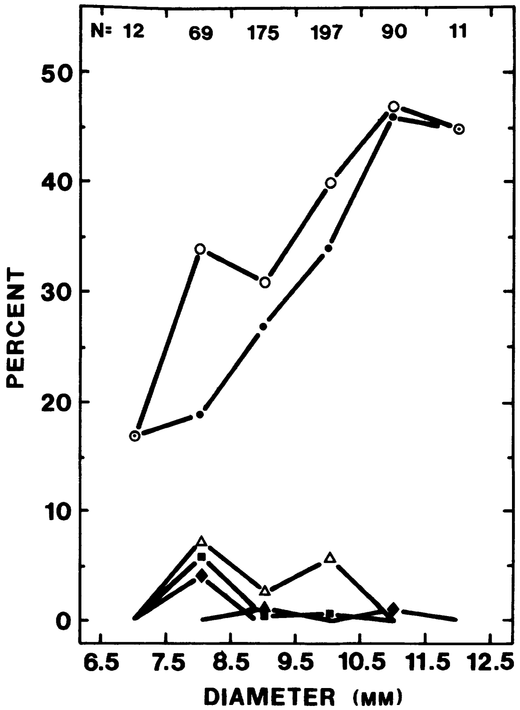

FIGURE 1. Percentage of patent trematode infections in *Helisoma anceps* relative to snail shell diameter. Snails were collected from Charlie's Pond on 20 October 1988. Key: (○) all species combined; (●) *Halipegus occidualis*; (△) *Megalodiscus temperatus*; (■) *Diplostomulum scheuringi*; (◆) ornatae-type cercariae; (▲) armatae-type cercariae; N, number of snails examined from each size class.

Mark retention

Snails marked in a manner similar to the released snails, but maintained in aquaria in the laboratory, retained marks for at least 4 mo. Similarly, snails recaptured in the cove until 12 July 1988 had recognizable marks.

Snail activity

Several searches from the cove shoreline were made prior to the first collection of overwintered snails on 23 March 1988, to count the number of marked snails visible above the pond bottom. These searches revealed that snails were active when water temperatures were above 8.5 C and that they remained active for at least 36 days

TABLE I. Categorization of recaptured *Helisoma anceps* according to assays in the fall and following spring for the presence of patent infections with *Halipegus occidualis*.

Month of recapture	Number of recaptures	% Infected	Infection category*			
			− −	− +	+ +	+ −
Mar 1988	29	34.5	15	1	9	4
Apr 1988	51	37.3	30	7	12	2
May 1988	12	66.7	4	5	3	0
Jun 1988	3	33.3	1	1	0	1

* (− −) not shedding cercariae in fall or spring assays; (− +) not shedding in fall assay, shedding in spring assay; (+ +) shedding in both fall and spring assays; (+ −) shedding in fall assay, not shedding in spring assay.

following initial release. Snails already had emerged from the substratum by the time the first spring search was made on 1 March 1988. The 2 greatest 1-day recoveries of marked snails during the postwinter collections were 29 on 23 March 1988 (water temp. = 17 C), and 25 on 14 April 1988 (water temp. = 23 C). All recaptured snails but 1 were recovered from 1 of the 5 sites at which they were released.

Parasitism in overwintered snails

During 1988, 86 marked snails were recaptured. Of these, 11 were recaptured twice, and 1, 3 times. In the fall collection, these 86 snails had been categorized as: 64.0% not shedding cercariae, 31.4% shedding *H. occidualis,* 3.5% shedding *M. temperatus,* and 1.2% shedding *D. scheuringi.* None that had been shedding ornatae or armatae cercariae was recaptured. These values were all within 2 percentage points of prevalences recorded in the 556-snail collection the previous fall.

Ten snails that shed cercariae in the fall sample were no longer shedding cercariae upon recapture. These included 2 of 3 snails that previously shed *M. temperatus* and the single snail that previously shed *D. scheuringi.* These snails were rereleased, but only 1 was recaptured a second time; this snail shed *M. temperatus* on 20 October 1987, did not shed any cercariae at the time of its first recapture on 26 May 1988, but was shedding *H. occidualis* at the time of its second recapture on 27 June 1988. Dissection revealed 11 sporocysts and 1,653 rediae of *H. occidualis* but no intramolluscan stage of *M. temperatus.* The other 7 snails that were no longer shedding cercariae upon recapture previously had shed *H. occidualis* in the fall collection. Five of these snails were dissected. In 4, gonads were intact and functional (eggs had been laid), and no parasite was found. The fifth had what appeared to be a new infection with *H. occidualis* because rediae were small, contained no cercariae, and were located primarily in the hepatopancreas.

Recruitment and loss of *H. occidualis* were examined using recapture data grouped by month (Table I), excluding from analysis those snails that shed cercariae other than *H. occidualis* in the prewinter collection. Sample sizes in several cells of Table I were too low to permit proper statistical testing for changing proportions of snails in different infection categories over time. However, certain aspects of infection dynamics are suggested by these data. First, examination of snails that were not shedding in the fall collection revealed that 6.7% were shedding cercariae in March, 18.9% in April, 55.6% in May, and 50.0% in June, indicating that new patent infections began appearing at about the time that snails emerged from the substratum. Second, several snails never shed cercariae at least through May and 1 of these into June. Third, 4 of 13 (30.8%) snails that had patent infections in the fall sample were no longer shedding cercariae at their emergence in March. Fourth, the similarity between fall prevalence and prevalence of *H. occidualis* in the first spring sample resulted from a combination of infection loss in some snails and the appearance of new infections in others.

Multiple recaptures

Multiple recapture data were obtained for 13 snails. One snail that had a patent infection with *M. temperatus* replaced by *H. occidualis* was described earlier. Data on the remaining 12 are presented in Table II. Three snails had patent infections at 2 recapture times spaced 22–37 days apart. Four snails were not shedding on successive recaptures spaced 22–51 days apart, although 1 of these was patent at the third recapture. One snail had become patent between the time of initial release and the first recapture, and it was still patent at the second recapture, 51 days later. Six snails that were not shedding at 1 recapture (23 March–26 May) had patent infections at subsequent recaptures that were made 14–51 days later.

Snail growth

Snails were recaptured at various times 155–250 days after first release. Diameters of 15 uninfected snails recaptured in the first postwinter collection (23 March 1988; day 155) were 2.6 ± 1.8% greater than their initial diameters (*t*-test

TABLE II. Status of infection with *Halipegus occidualis* in 12 multiply recaptured *Helisoma anceps*.

Initial status	First recapture	Second recapture	Third recapture
+ 26 Oct 1987*	+ 23 Mar 1988	+ 14 Apr 1988	
+ 26 Oct 1987	+ 23 Mar 1988	+ 14 Apr 1988	
+ 26 Oct 1987	+ 5 Apr 1988	+ 12 May 1988	
− 26 Oct 1987	+ 5 Apr 1988	+ 26 May 1988	
− 26 Oct 1987	− 23 Mar 1988	+ 14 Apr 1988	
− 26 Oct 1987	− 23 Mar 1988	+ 12 May 1988	
− 26 Oct 1987	− 14 Apr 1988	+ 12 May 1988	
− 26 Oct 1987	− 20 Apr 1988	− 26 May 1988	+ 27 Jun 1988
− 26 Oct 1987	− 12 May 1988	+ 26 May 1988	
− 26 Oct 1987	− 23 Mar 1988	− 14 Apr 1988	
− 26 Oct 1987	− 23 Mar 1988	− 21 Apr 1988	
− 26 Oct 1987	−5 Apr 1988	− 26 May 1988	

* Shedding (+) or not shedding (−) cercariae; date of assay.

of H_0, $\mu = 0\%$, vs. H_1, $\mu > 0\%$: $t = 5.59$, df = 14, $P < 0.001$).

Recapture weights of uninfected snails (not shedding cercariae initially or at recapture) were described by the relationship:

$W2 = 134 + 0.959W1 - 1.64T + 0.00568T^2$ (n = 51, $R = 0.98$, $P < 0.001$). Snails shedding cercariae of *H. occidualis* initially and at recapture had similar observed and predicted recapture weights (12 heavier than predicted, 11 lighter: $\chi^2 = 0.04$, $P = 0.84$). Snails that shed cercariae of *H. occidualis* initially, but not at recapture, also had similar observed and predicted recapture weights (3 heavier than predicted, 4 lighter: $\chi^2 = 0.14$, $P = 0.71$). Snails that were not shedding initially, but that shed cercariae of *H. occidualis* at recapture, were lighter than predicted at recapture (3 heavier and 10 lighter than predicted, 1 tied with predicted weight: $\chi^2 = 3.76$, $P = 0.05$).

DISCUSSION

Seasonal changes in the proportion of infected hosts, or in the mean number of parasites per infected host, are the most frequently obtained data in studies on the population dynamics of parasitic infections. Although these data permit quantification of changes in parasite population size, they may be inadequate for discerning underlying processes, particularly when several opposing processes are involved. The use of a mark–recapture method in the present study provided strong evidence that the apparent constancy of fall and spring prevalences of *H. occidualis* in *H. anceps* reported by Crews and Esch (1986) was a net effect of at least 3 processes: loss of established infections, recruitment of new infections, and replacement of infections with 1 trematode species by another.

Loss of infection

The disappearance of infected hosts from the population can occur by mortality of infected hosts or by loss of infections. It is likely that there was extensive mortality among marked snails, as only 17% were ever recaptured. Maximum 1-day, postwinter collections of 29 and 22 marked snails per day, when compared with the 38–49 sightings made per day on 3 fall collections, provides a crude estimate that about 50% of the marked snails died during the winter. The fate of the remaining snails is unknown. Movement out of the cove can be discounted because all but 1 of the marked snails were recaptured within a few meters of the point of release. This indicates that individuals of *H. anceps* show considerable site fidelity. Thus, infections are not acquired by moving over large areas of littoral vegetation, but by differential distribution patterns of parasite eggs within different sites in the cove. Moreover, observations on the condition of markings suggest that mark loss was inconsequential during the earlier spring collections.

Although extensive mortality of *H. anceps* clearly occurred, there was no evidence of disproportionate mortality among parasitized snails. Wright (1966) noted that trematode infection increases the susceptibility of many snails to stress, but that significant mortality effects in natural populations had not been demonstrated. Individual marking allowed us to identify changes in infection status that would otherwise confound interpretations based on a before-and-after sampling procedure, and permitted us to conclude that snails infected with various species of trematodes in the fall assay were recovered the following spring in the same proportions.

Rediae of *H. occidualis* completely consume gonadal tissue of *H. anceps* (Crews and Esch, 1987). Therefore, the recapture of snails that had recovered from infection with *H. occidualis* and repaired the gonad was surprising. Although our results also could have arisen because of initial false-positive classifications, we dismiss this on the grounds that our randomly selected control group had no false positive, and that, during 3 yr of routine monitoring of *H. anceps* in Charlie's Pond, no false positive occurred among hundreds of snails examined using the same methods. Self-cure and reversal of indirectly caused castration are known for infections with trematodes lacking redial stages (Cheng and Snyder, 1962; Etges and Gresso, 1965), but study on trematodes with rediae that cause direct gonad damage suggest that castration is permanent; if healing occurs it is extremely rare (Hodasi, 1972; Sousa, 1983). Our results not only demonstrated reversal of parasitic castration, but indicate that it may be common. We do not know when gonadal repair occurred, but because there was significant growth of *H. anceps* in Charlie's Pond between 23 October 1987 and 23 March 1988, it is likely that environmental conditions also would have been conducive to other anabolic processes, such as repair. It is also possible that rediae are more vulnerable during cold temperatures when cercarial shedding ceases, allowing the host to respond effectively. Additional mark-recapture and laboratory studies currently are underway to evaluate more fully this intriguing phenomenon of castration reversal.

Recruitment

The mark-recapture method allowed us to identify new infections, i.e., those that recently became patent, in snails collected in the spring. Some of these may represent the maturation of prepatent infections from the previous October. Based on the fall determination that 10.8% of nonshedding snails had prepatent infections with *H. occidualis,* it is probable that some snails in March represent the maturation of infections acquired the previous fall.

By April, the frequency of recently acquired infections was high enough that it could not be accounted for solely by postulating maturation of prepatent infections. Therefore, some of those snails had infections that were acquired after their initial release. We can deduce also that at least some of the patent infections in overwintered snails resulted from acquisition of parasite eggs after the snail's emergence from the substratum in the spring. At 20 C, *H. occidualis* becomes patent 6 wk after infection (T.M.G., A.W.S., unpubl. data). Water temperature in Charlie's Pond reached 20 C by mid-April. Multiple recaptures of 3 snails (Table II) indicated onsets of patency after 14 April, 12 May, and 26 May; these infections were acquired presumably by ingestion of eggs no earlier than about 3 March, 31 March, and 14 April, respectively. We know that snails began emerging from the substratum by 1 March. One source of these infections may have been overwintered eggs, as green frogs do not emerge from hibernation at Charlie's Pond until mid-April. Macy et al. (1960) reported that eggs of *H. occidualis* maintained at 4 C for 28 mo exhibited a hatching response similar to freshly laid eggs.

An electrophoretic study of *H. anceps* in Charlie's Pond by Mulvey et al. (1987) showed allozyme differences between uninfected and *H. occidualis*-infected snails, and suggested that a subpopulation of snails may possess genetically based resistance. Rapid increases in the prevalence of *H. occidualis* in young-of-the-year *H. anceps* (Crews and Esch, 1986) suggest that exposure rates to the parasite are high. In the present study, 5 of 11 overwintered snails captured in May and June, and presumably born before the previous September (Crews and Esch, 1986), were still not shedding.

Antagonism among trematode species

Interspecific antagonism among trematodes in snails is well documented by field and laboratory studies (Lim and Heyneman, 1972; Kuris, 1989; Sousa, 1989). Our documentation (via multiple recaptures) of the replacement of an infection with *D. scheuringi* by 1 of *H. occidualis* provides field evidence of an antagonistic interaction (*H. occidualis* > *D. scheuringi*) and suggests at least 1 route by which the high prevalence of *H. occidualis* may affect the trematode infracommunities and component trematode communities of *H. anceps.*

An intriguing observation was that non-*H. occidualis* infections tended to occur in smaller *H. anceps* than those harboring *H. occidualis.* Trematodes may parasitize restricted size ranges of snails for reasons unrelated to interspecific antagonism (Sousa, 1983; Lauckner, 1984), but our analysis showed that even if different host-size preferences exist between *H. occidualis* and other trematode species, there were still fewer multiple infections than expected. Crews and Esch (1986) also reported an absence of multiple infections in 806 *H. anceps* from Charlie's Pond. The existence of antagonistic interactions provides 1 explanation for the absence of multiple infections. However, it is premature to speculate on the dynamics of these interactions, as experimental infections to establish host size preferences and identify dominance hierarchies (sensu Kuris, 1989; Sousa, 1989) among the larval trematodes of Charlie's Pond remain to be done.

Snail growth

Although we confirmed the observation of Crews and Esch (1986) that *H. anceps* infected with *H. occidualis* were significantly larger than uninfected snails, our data contradict their suggestion that gigantism occurred in snails following infection. Gigantism occurs when energy normally allocated to reproduction is diverted toward somatic growth (Sousa, 1983; Minchella, 1985). Our mark–recapture method showed that gigantism did not occur, as snails with preexisting infections grew similar to, and snails with new infections grew less than, uninfected snails of similar initial size. Previous mark–recapture studies (Bourns *in* Wright, 1971; Sousa, 1983) reported reduced growth in infected snails but did not report separate results for recent vs. older infections.

Many processes other than direct effects on growth can produce a correlation between host size and parasite prevalence that may be misinterpreted as gigantism (Baudoin, 1975; Sousa, 1983). These include reduced mortality rates in older infected hosts or increased mortality rates in younger infected hosts, a tendency to infect larger hosts, and accumulation of infections over time in a host that grows as it ages. Our data were insufficient to address the question of size-specific mortality. There is probably a greater exposure of larger *H. anceps* to *H. occidualis,* as transmission is via ingestion of eggs. Moreover, the infections are long-lived in most hosts, so older hosts probably accumulate infections.

Overwinter dynamics

Laboratory experiments by Crews and Esch (1986) showed that cercarial release from *H. anceps* infected with *H. occidualis* ceases in sub-12 C water, such as occurs from November to March in Charlie's Pond, while snails hibernate. The present study indicates that the host–parasite relationship is far from quiescent during the overwintering period. Prepatent infections mature. Existing infections may be lost and either be replaced by a different species or be followed by healing of snail gonadal tissues. Therefore, the observation of no net change in parasite prevalences among overwintering *H. anceps* reflects a dynamic balance between some processes that tend to increase prevalence and others that tend to decrease it.

Perhaps 1 of the most significant processes that this mark–recapture study revealed is reversal of parasitic castration. If there is a genetic component in the susceptibility of *H. anceps* to *H. occidualis* (Mulvey et al., 1987), the continuous high prevalence of *H. occidualis* in Charlie's Pond suggests the existence of mechanisms retarding the spread of resistant genotypes. Healing would reduce the selective pressures against susceptible genotypes, because once infected, a proportion of individuals possessing susceptible genotypes could continue to make a reproductive contribution.

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