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Author(s): Derek A. Zelmer and Gerald W. Esch

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## RELATIONSHIP BETWEEN STRUCTURE AND STABILITY OF A *HALIPEGUS OCCIDUALIS* COMPONENT POPULATION IN GREEN FROGS: A TEST OF SELECTIVE TREATMENT

Derek A. Zelmer\* and Gerald W. Esch

Department of Biology, Wake Forest University, Winston–Salem, North Carolina 27109

**ABSTRACT:** The aggregated nature of helminth parasite populations has led to the suggestion that selectively treating heavily infected hosts can efficiently reduce parasite abundance and morbidity within a host population. Moreover, it has been postulated that a selective treatment protocol might have long-term effects on parasite transmission by disrupting the stability attributed to aggregated parasite population distributions by theoretical models. Long-term investigation has demonstrated year-to-year consistency in the population dynamics of *Halipegus occidualis* in green frogs from Charlie's Pond, North Carolina. In 1996, removal of all but 1 worm from each frog with  $\geq 15$  worms reduced the estimated component worm population by 45%, thereby decreasing mean intensity and aggregation (variance-to-mean ratio) of *H. occidualis* in the frogs by 85% and 63%, respectively. The following year, mean intensity, aggregation, and host colonization trends returned to pretreatment levels, indicating no effect of worm removal and demonstrating the stability of this host–parasite system. Although this result might be attributable to inefficient treatment or the presence of infection reservoirs, it is suggested that parasite population stability in this system might be governed by prevalence rather than intensity of adult worms. Therefore, repeated selective treatment might effectively modify intensity-dependent morbidity in similar host–parasite systems but should not affect further parasite transmission.

Systems demonstrating long-term constancy in population abundance, or community richness, often are referred to as stable. Stability, however, strictly indicates the tendency of a system to return to an equilibrium point following perturbation. Thus, the true test of whether or not a biological system is stable, as opposed to merely persistent, is to disturb it sufficiently to alter the characteristic of interest and measure the response over 1 complete turnover of all individuals (Connell and Sousa, 1983). Parasite populations can exhibit both constancy (Smith, 1973; Kennedy and Rumpus, 1977; Kennedy and Burrough, 1981) and stability (Janovy et al., 1997), in some instances with markedly low long-term variation in population sizes relative to free-living animals (Connell and Sousa, 1983). In particular, helminth parasites of humans exhibit remarkable temporal stability (Anderson, 1979; Anderson and May, 1985) with prevalences and abundances that return to precontrol levels within 1 yr of anthelmintic treatment (Arfaa and Ghadirian, 1977; Croll et al., 1982; Holland et al., 1989).

Theory suggests that aggregated parasite distributions (Crofton, 1971a) have a stabilizing influence on parasite populations through regulation of host populations mediated by death of heavily infected hosts (Crofton, 1971b; Anderson and May, 1978) or through concentration of density-dependent effects on parasite infrapopulations (Shaw and Dobson, 1995). Although robust in terms of mathematical models, there is little empirical evidence that the scale of parasite-induced mortality is responsible for regulation of natural host–parasite systems (Bradley, 1974).

The characteristic return of human helminth abundances to pretreatment levels has inspired treatment protocols concentrating on host populations as a whole rather than on individuals, with a concomitant shift in treatment objectives from control of incidence to a reduction in morbidity (Anderson and May, 1982, 1985; Anderson and Medley, 1985). Population-level protocols fall into 3 basic categories, i.e., mass, selective, and targeted treatment. Mass treatment involves drug therapy for all

consenting members of a population. Selective treatment (Smillie, 1924) exploits parasite aggregation by concentrating therapy on heavily infected individuals. Thus, a relatively small number of individuals will require treatment in order to substantially impact morbidity and, in theory, transmission (Anderson and Medley, 1985). Targeted treatment is a variation on the selective protocol in which efforts are concentrated on susceptible groups as defined by age, sex, religion, or some behavioral attribute (Asaolu et al., 1991). On a per treatment basis, more parasites should be removed by selective treatment; however, the requisite cost of continual pretreatment identification of heavily infected individuals is great enough to be prohibitive (Holland et al., 1996).

Although the utility of these procedures has been modestly evaluated in treatment of human populations (Warren and Mahmoud, 1976; Mahmoud et al., 1983; Asaolu et al., 1991; Holland et al., 1996), the use of humans in study protocols is fraught with difficulties, ranging from ethical considerations to the use of indirect methods to determine prevalence and abundance of infection (Anderson and May, 1985). Difficulty also arises in partitioning observed reductions in worm burdens between the immediate effects of treatment and any resultant long-term disruption of parasite transmission. The present investigation tests the effect of selective treatment on the stability of a well defined host–parasite system that is conducive to accurate enumeration of parasite intensity and examines the role of aggregation or other possible factors in promoting parasite component population stability.

The hemiurid trematode *Halipegus occidualis* inhabits the buccal cavity of green frogs (*Rana clamitans*), thus facilitating repeated measures of worm abundance in the field without harm to the host by a visual census of worm burden. The life cycle of *H. occidualis* involves 4 hosts. Eggs shed by the adult worm and ingested by pulmonate snails (*Helisoma anceps*) release miracidia that proceed through sporocyst and redia stages, resulting in the release of cystophorous cercariae onto the pond substratum (Krull, 1935). Feeding activities of ostracods (*Cypridopsis* sp.) lead to the penetration of their gut wall by a delivery tube from the cercariocyst, ensued by delivery of the cercaria into the ostracod hemocoel (Goater et al., 1990). Ingestion of infected ostracods by odonate naiads bridges the tro-

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\* Current address: Division of Biological Sciences, Emporia State University, Emporia, Kansas 66801

TABLE I. Total number of green frog individuals captured and total number of captures (including recaptures) for April–August of 1992–1997.

| Year | Sample size<br>(captures : frogs) |       |       |       |        |
|------|-----------------------------------|-------|-------|-------|--------|
|      | April                             | May   | June  | July  | August |
| 1992 | NS*                               | 7:7   | 41:30 | 44:31 | 25:21  |
| 1993 | 11:9                              | 25:19 | 30:21 | 19:16 | 5:5    |
| 1994 | 24:20                             | 13:11 | 17:12 | 14:13 | 10:8   |
| 1995 | 9:8                               | 17:17 | 21:18 | 19:17 | 19:14  |
| 1996 | NS*                               | 20:11 | 49:35 | 35:25 | 15:9   |
| 1997 | 0:0                               | 0:0   | 23:19 | 36:26 | 11:10  |

\* NS = not sampled.

phic gap between ostracods and frogs, as green frogs become infected by consumption of odonate hosts (Zelmer and Esch, 1998a).

Transmission dynamics in this host–parasite system have been the subject of long-term investigation in a small North Carolina pond since 1983 (Esch et al., 1997). Seasonal patterns of prevalence and abundance in green frogs have remained remarkably constant since 1992, despite fluctuations in frog population size (Table I; Zelmer et al., 1999). Seasonality of transmission in this system is mediated, in part, by the ecology of the snail hosts. The *H. anceps* population turns over annually, with the previous year's cohort dying off and being replaced between June and August of each year (Crews and Esch, 1986; Fernandez and Esch, 1991a). Prevalence of *H. occidua* in snail hosts follows an annual trend closely associated with this cycle (Fernandez and Esch, 1991b; Sapp and Esch, 1994). Adults of *H. occidua* can overwinter in frog hosts but are lost early the following breeding season (Goater, 1989; Wetzel and Esch, 1996a). It is also believed that yearly emergence of odonate naiads creates an annual turnover of *H. occidua* metacercariae (an assumption that will be examined in this investigation) as does the more frequent, but asynchronous, turnover of ostracods. Thus, the known biology of the hosts and parasites indicates that the minimum time period to observe a response to perturbation in this system, i.e., 1 complete turnover of the *H. occidua* suprapopulation, is 1 yr.

The goal of selective treatment of adult green frogs in Charlie's Pond was the removal of approximately 50% of the adult worm component population. This was to be accomplished by removing worms only from frogs with large infrapopulations, leaving 1 worm in each treated frog so as not to compound the effects of reduced abundance or worm aggregation with that of decreased prevalence. Annual turnover in this system facilitates the separation of direct treatment effects on abundance from the effects on the following year's parasite colonization, thus providing insight into the stability of this host–parasite system. If the basic tenets of selective treatment are valid, this reduction in intensity, even with constant prevalences, should have a negative impact on *H. occidua* transmission.

## MATERIALS AND METHODS

This investigation was conducted in Charlie's Pond, a 2-ha, spring-fed impoundment in Stokes County, North Carolina (Esch et al., 1997). Green frogs were sampled weekly from May through October in 1992

and 1996, from April through October in 1993–1995, and from April through August in 1997. Frogs were captured by hand from both water and shore by wading or from an inflatable raft. All collecting was done at night with the use of a head lamp. Mouths of captured frogs were opened with forceps and examined for *H. occidua*. Accurate counts of large infrapopulations were facilitated by temporary removal of adult worms, as the parasites do not appear to be affected adversely by removal or replacement (Krull, 1935). Individual frogs were marked for identification by toe clipping (Martof, 1953) and returned to their site of capture. Monthly mean intensities and variance-to-mean ratios were generated by weighting intensity by the number of times a frog was captured. The number of individual frogs captured and the total captures for each month are presented in Table I.

From June through September of 1995, libellulid (Odonata: Anisoptera) and coenagrionid (Odonata: Zygoptera) naiads were collected monthly from reed beds within Charlie's Pond, taken to the laboratory, and isolated in 60-ml plastic dishes. Within 1 wk of collection, the midgut was removed from each naiad and examined for *H. occidua* metacercariae.

In 1996, an attempt was made to remove 50% of the component parasite population by removing worms from only heavily infected green frogs. One worm was left in each treated frog so as not to affect prevalence. Initial estimates of the number of frogs to treat were derived from *H. occidua* population data for 1995. A negative binomial model fit to parasite distribution data ( $n = 54$  frogs) using method 1 of Anscombe (1950) proved an adequate description of observed counts based on the  $U$ -statistic goodness of fit test (Evans, 1953) and the chi-square test ( $P > 0.50$ ). A Poisson distribution did not adequately describe the frequency distribution (chi-square test;  $P < 0.001$ ).

Green frog population size was estimated using a modified Jolly–Seber method (Zelmer et al., 1999) and multiplied through negative binomial probabilities (Anscombe, 1950) to produce an estimate of worm population size. These calculations were repeated in June, July, and August of 1996 using current parasite population data (maximum abundance for each individual frog) to monitor the number of frogs to be treated and the number of worms to be removed. In late June of 1996, sampling was conducted each night for 1 wk in order to generate a closed model estimate of frog population size (model  $M_h$  of Otis et al., 1978) that was used to further modify removal estimates.

Frog intensities were monitored continuously and worms removed from all heavily infected frogs (according to the above criteria) captured from April through September of 1996. Worms colonizing treated frogs after initial worm removal also were removed as encountered to maintain an intensity of 1 worm in treated frogs. Initial estimates based on frog and parasite population data from 1995 suggested that 49.0% of the worm population (164 worms) could be removed from 14.5% of the host population (7 frogs) by the removal of all but 1 worm from frogs with infrapopulations greater than 15 worms. Final estimates for 1996 generated by fitting the observed ( $n = 57$  frogs) frequency distribution (Fig. 1) to the estimated population size ( $84 \pm 15$  frogs) indicated that treatment of 8 frogs (10.7% of the total population) would result in the removal of 208 worms, which was half the estimated parasite population size. In all, 191 worms were removed from a total of 8 green frogs or 45.9% of the estimated worm population. The capture histories of the 8 treated frogs are presented in Table II. In addition, 19 of 20 observed worms were removed from the single pickerel frog (*Rana palustris*) captured in 1996.

Of the 191 worms removed from green frogs, 31 (16.2%) were juveniles; 23 (14.4%) of the 160 adults removed were known to have matured within the preceding 2 wk. Fifty (31.3%) of the adults removed had been gravid for less than 1 mo, and a further 40 worms (25.0%) had matured within the previous 1.5 mo. We were unable to estimate the age of 47 (29.4%) of the adult worms.

For the sake of comparison, in 1996, 2 separate mean intensities were calculated for each month. The first included only those worms present after worm removal, i.e., removed worms were subtracted from observed intensities. All worms that established in an individual frog, including those that had been removed, were factored into the second calculation. The difference between these 2 mean intensities is a measure of the proximal effect of worm removal. The effects of treatment on *H. occidua* recruitment the following year (1997) were analyzed by comparing mean abundance (averaged for individual frogs each month) to 1993–1995 mean abundances using ANCOVA with the av-

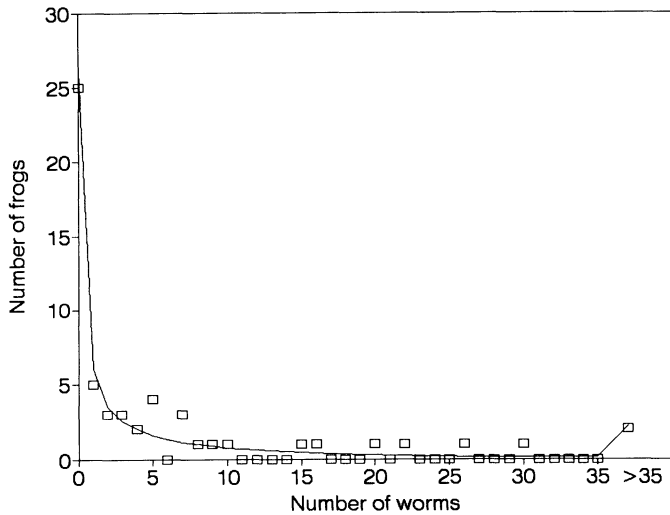


FIGURE 1. Frequency distribution of *Halipegus occidualis* abundance in green frogs from Charlie's Pond, 1996. Solid line represents the fit of the data to a negative binomial model using method 1 of Anscombe (1950).

erage mean daily temperature for each month as a covariate. Mean daily temperature was used because of an unusually cold spring in 1997. Data from August 1993–1995 were excluded because the decline in parasite abundances in late summer is related to factors other than temperature, i.e., worm senescence, odonate eclosure, and frogs dispersing from the pond. This exclusion does not affect interpretation of the analysis because the variable of interest is parasite recruitment. Temperature data were obtained from the State Climate Office of North Carolina (station 313630, approximately 20 km southwest of the pond). Use of ecological terms follows the recommendations of Bush et al. (1997).

**RESULTS**

Observations on libellulid naiads from Charlie's Pond in 1995 indicate this population turns over in August, as evidenced by a sharp decrease in average odonate head diameter and concurrent decline in prevalence of *H. occidualis* metacercariae in the naiads (Fig. 2). Only 24 coenagrionid naiads were collected in 1995, but, based on mean head diameter, this population appeared to turn over between August and September (data not shown). Whereas 12 of 14 coenagrionids captured in June and July of 1995 harbored *H. occidualis* metacercariae, none of the 10 captured in August and September was infected.

In the odonate naiad population, cohort replacement occurs after the snail population has turned over (Fig. 3). Thus, the majority of infections in the new naiad cohort originate from infections established in the new snail cohort and are probably recruited the following spring. The timing of odonate turnover also follows the peak period of frog colonization by *H. occidualis* (Fig. 3) and, therefore, colonization of frogs is the result of ingesting infected naiads from the previous year's cohort.

A comparison of monthly mean intensities of *H. occidualis* including only those worms remaining after treatment with those that included removed worms in the component population (Fig. 4A) demonstrates that a consistent pattern of relatively low mean intensities was maintained by continual removal. The difference between these 2 estimates provides an indication of the number of worms removed each month. Worm removal produced a similar effect on the variance-to-mean ratio

TABLE II. Capture histories, observed infrapopulations, and worms removed for the 8 green frogs treated in Charlie's Pond in 1996.

| Host number | Date | Number of worms (adults/ juveniles) | Number removed (adults/ juveniles) |
|-------------|------|-------------------------------------|------------------------------------|
| G40         | 6/30 | 2/7                                 | 0/0                                |
|             | 8/2  | 29/0                                | 28/0                               |
|             | 8/13 | 1/0                                 | 0/0                                |
| G202        | 8/19 | 1/0                                 | 0/0                                |
|             | 6/27 | 15/4                                | 14/4                               |
|             | 6/28 | 1/0                                 | 0/0                                |
| G240        | 7/3  | 1/3                                 | 0/3                                |
|             | 5/25 | 6/0                                 | 0/0                                |
|             | 5/30 | 7/0                                 | 0/0                                |
|             | 6/20 | 10/4                                | 10/3                               |
|             | 6/27 | 1/0                                 | 0/0                                |
|             | 7/2  | 1/0                                 | 0/0                                |
|             | 7/3  | 1/2                                 | 0/2                                |
| G254        | 7/17 | 1/0                                 | 0/0                                |
|             | 5/8  | 0/0                                 | 0/0                                |
|             | 5/16 | 0/0                                 | 0/0                                |
|             | 5/30 | 0/2                                 | 0/0                                |
|             | 7/1  | 11/4                                | 10/4                               |
| G266        | 7/24 | 8/4                                 | 7/4                                |
|             | 6/20 | 3/7                                 | 0/0                                |
|             | 6/28 | 10/4                                | 9/4                                |
|             | 8/19 | 27/0                                | 26/0                               |
| G290        | 9/9  | 0/0                                 | 0/0                                |
|             | 7/2  | 0/0                                 | 0/0                                |
|             | 7/17 | 0/12                                | 0/0                                |
| G291        | 8/3  | 17/3                                | 16/3                               |
|             | 7/17 | 27/4                                | 26/4                               |
| G294        | 7/24 | 0/3                                 | 0/0                                |
|             | 9/18 | 15/0                                | 14/0                               |

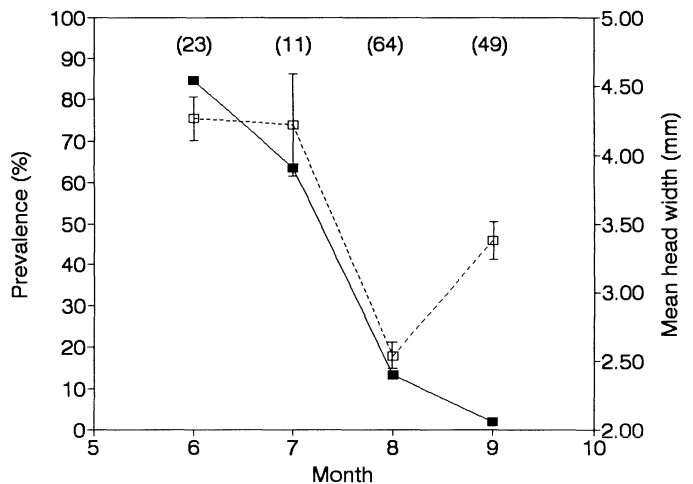


FIGURE 2. Temporal changes in *Halipegus occidualis* metacercariae prevalence (filled boxes, solid line), and mean head width  $\pm$  SE (open boxes, broken line) of libellulid naiads in Charlie's Pond, 1995.

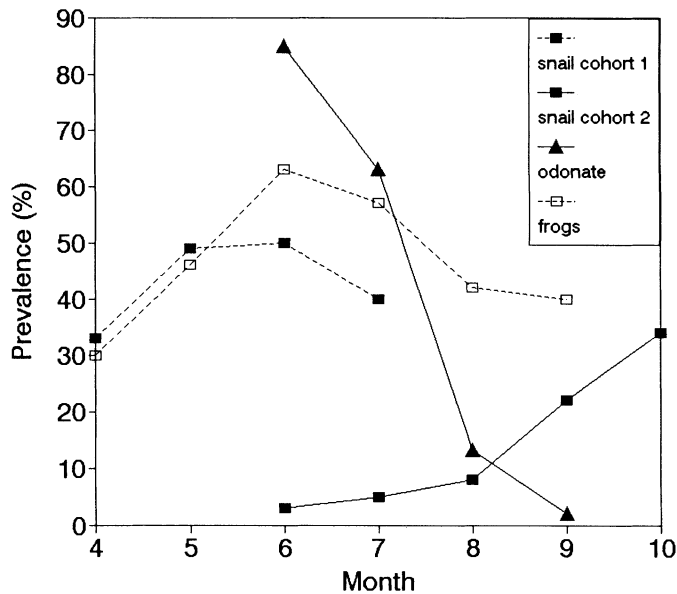


FIGURE 3. Turnover of *Halipegus occidialis* populations in snail (1989), odonate (1995), and green frog (1992–1995) hosts in Charlie's Pond. Snail prevalence data from Fernandez and Esch (1991b).

of worm population estimates, thus maintaining low levels of aggregation relative to those estimated from the inclusion of removed worms in the calculation (Fig. 4B).

The population dynamics of *H. occidialis* in green frogs the year following removal (1997) was similar to that observed 3 yr prior to worm removal (Fig. 5), with the exception of a temporal shift of the curve. The mean daily temperatures in the spring of 1997 were lower than those of the preceding 4 yr, and frogs were not observed in the pond until June of that year. Model I regression analysis demonstrated a significant positive relationship between frog activity (measured as the average number of frogs caught per night as a proportion of the maximum monthly average for each year) and average daily temperature ( $F = 26.06$ ;  $P < 0.0001$ ;  $r^2 = 0.62$ ).

To compare the population dynamics of *H. occidialis* in 1997 to that observed in 1993–1995, ranked abundances (averaged for each individual frog within each month) were compared among years using ANCOVA with the average daily temperature for each month as a covariate. Temperature was significantly correlated with ranked worm abundance ( $F = 21.92$ ;  $P < 0.0001$ ;  $r^2 = 0.094$ ) and did not interact with year in its effects ( $F = 1.37$ ;  $P = 0.25$ ). When mean daily temperature was controlled for as a covariate, there were no significant differences in worm abundance between 1997 and 1993–1995 ( $F = 0.99$ ;  $P = 0.40$ ). Thus, the slope and elevation of the relationship between temperature and worm abundance were not affected by the removal of worms in 1996, indicating that treatment did not have an effect on the 1997 population dynamics of *H. occidialis* in green frogs relative to the preceding years.

## DISCUSSION

The temporal shift in the population dynamics of *H. occidialis* in Charlie's Pond in 1997 relative to preceding years might be interpreted as an effect of the worm removal. When changes in abundance are related to mean daily temperature

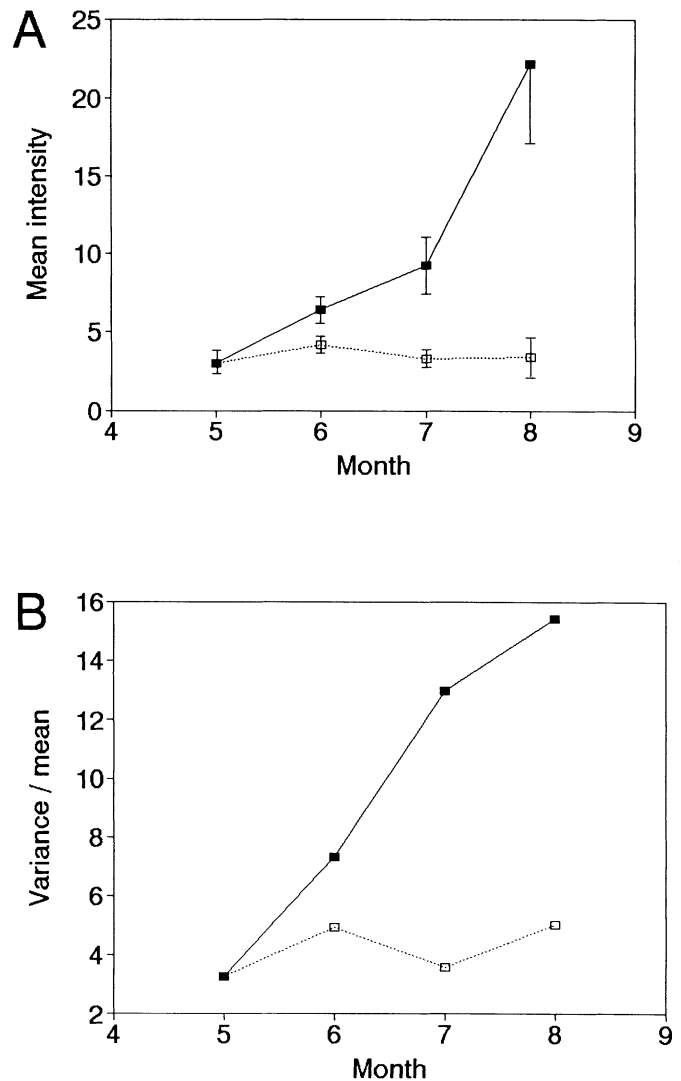


FIGURE 4. Changes in *Halipegus occidialis* population parameters in green frogs as the result of treatment. Filled boxes indicate calculations including removed worms and subsequent recruitment; open boxes indicate calculations including only worms remaining in the pond after treatment. (A) Mean intensity  $\pm$  SE. (B) Aggregation as measured by variance-to-mean ratios.

rather than month, however, this difference is lost, suggesting that the shift was due to an unusually cold spring in 1997. Thus, despite the reductions in abundance and aggregation in 1996, selective treatment of frogs in Charlie's Pond did not affect the degree or dynamics of infection of adult frogs by *H. occidialis* the following year. This result has 3 potential explanations: insufficient or ineffective worm removal, compensation by reservoirs of infective stages, or transmission mechanisms that are more reliant on infection prevalence than they are on infection intensity. Although each scenario will be addressed separately, it is important to note that none of these explanations is mutually exclusive.

### Insufficient worm removal

Although the data suggest that the size of the worm component population was substantially altered, this reduction can-

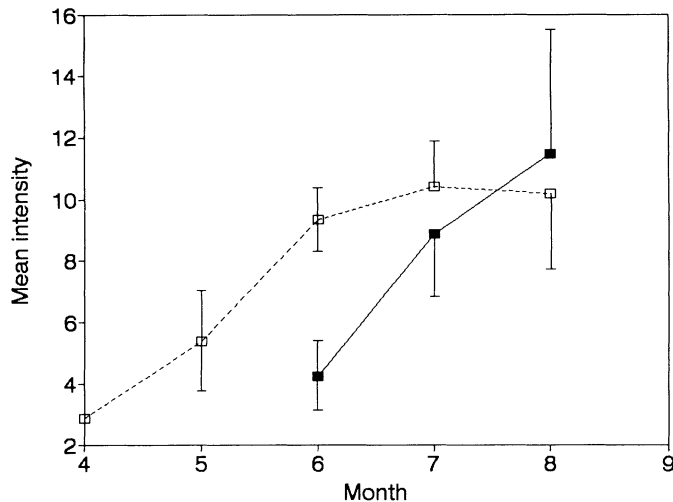


FIGURE 5. The effect of worm removal on the following year's population dynamics for *Halipegus occidualis* in Charlie's Pond. Combined mean intensity  $\pm$  SE for 1993–1995, open boxes; 1997 mean intensity  $\pm$  SE, filled boxes.

not be translated directly into a decrease in egg production. Only 16.2% of removed worms were juveniles. All other removed worms were gravid adults that contributed eggs to the infective pool. Although we consider it unlikely that this egg production would have been sufficient to compensate for the worm removal, the argument that the reduction in egg production was less than the reduction in the worm population remains valid.

### Reservoirs of infection

Reservoirs of infection in intermediate hosts contribute to the stability of host–parasite systems (Anderson, 1974). Our results suggest that the component populations of *H. occidualis* in Charlie's Pond arise as distinct cohorts. Synchronous cohort replacement (turnover) occurs in the snail population during the period when adult worms are being recruited by, and are present in, frogs (Crews and Esch, 1986; Fernandez and Esch, 1991a). Thus, subsequent infection of the new snail cohort arises from frogs infected that season. The fact that the libellulid and coenagrionid naiad cohorts, the primary paratenic hosts for *H. occidualis* (Wetzel and Esch, 1996b), turn over after the snail cohort has been replaced suggests that the source of infection for the new naiad cohort arises from infections originating in the new snail cohort. Moreover, the timing of odonate naiad turnover indicates that frogs obtain their infections by ingesting naiads infected by the previous year's parasite cohort. In short, the synchronous turnover of both snail and odonate naiad populations suggests that frogs ingest metacercariae that developed from eggs shed the previous year.

Although the presence of discrete cohorts of *H. occidualis* in Charlie's Pond is a valid generalization, there are 2 possible reservoirs of infection that could serve as a link between cohorts, resulting in overlapping generations. Eggs of *H. occidualis* have been shown to respond to hatching stimuli after 28 mo of storage at 4 C (Macy et al., 1960). Although there would be loss due to sedimentation, and the duration of egg viability at higher temperatures is not known, the possibility that eggs

could persist the necessary 8–12 mo to overlap the following year's cohort cannot be ignored. Moreover, transmission of *H. occidualis* in Charlie's Pond is concentrated in areas where the distribution of the 4 hosts overlap (Zelmer et al., 1999). Accumulation of eggs would serve to maintain these foci and, therefore, transmission of the worm.

The second potential reservoir represents a link between cercariae produced by year-old snails and the new odonate naiad cohort. Given the time frame between snail turnover and odonate naiad turnover, coupled with the limited duration of infectivity of cercariae at summer water temperatures (Wetzel and Esch, 1995), it is unlikely that the cercariae themselves could provide this link. Persistent infections in ostracod hosts, however, could conceivably transfer the preceding year's metacercariae into the current year's naiad population. Although laboratory populations of infected ostracods do not survive for longer than 5 wk, development of *H. occidualis* metacercariae within ostracods requires 4 wk at 22 C (Zelmer and Esch, 1998b), suggesting that in the field, infected ostracods should survive long enough to infect young-of-the-year naiads.

### Relative importance of prevalence versus intensity

It is also possible that observed stability could be independent of parasite intensity and aggregation. Asexual reproduction of *H. occidualis* within snail hosts allows a snail infected by a single miracidium to produce as many cercariae as one infected by several miracidia. Thus, egg encounter per se, not the number of eggs encountered, is the only predictor of the production of cercariae that drives transmission in this system. It is the encounter of frog feces containing eggs rather than individual eggs that represents the fundamental spatial unit of infection for snails. The egg's long filaments cluster eggs within the frog feces (D. Zelmer, pers. obs.) and it is, therefore, the distribution of frog feces that determines snail infection probabilities. The site fidelity of the frog hosts (Zelmer et al., 1999) dictates that the distribution of these packets of infectivity is dependent upon the number of infected frogs within the pond and not the intensities of the individual infections. Moreover, the limited mobility of the intermediate hosts in the pond (Zelmer et al., 1999) suggests that subsequent infection of these hosts, and the infection of nearby definitive hosts, also depend on the distribution of the infective packets. Thus, the focal (fecal?) nature of transmission in this system suggests that colonization of hosts by *H. occidualis* will not be altered without a substantial decrease in infection prevalence in green frogs.

Failure to disrupt parasite transmission through treatment is an indication that the parasite population was not reduced below some threshold value. This theoretical value is determined by the number of sexually mature offspring produced by each female worm (Medley, 1994) and must fall below unity in order for parasite populations to decline. The concept of prevalence-based parasite transmission, however, suggests that for parasites with immotile infective stages, the number of offspring reaching maturity is dependent upon the number of infective packets in the environment. Thus, the threshold value of interest in these systems is not measured by worm population size but by the number of infective packets, i.e., the number of infected hosts. A frog with 1 gravid worm will produce as many infective fecal packets as a frog with many worms and, therefore,

all infected hosts contribute equally to the dispersal of infective packets in the environment. It is suggested that the failure of selective treatment in Charlie's Pond is not the result of insufficient worm removal but rather the failure to decrease the number of infective packets being dispersed by infected frogs.

Clearly a reciprocal experiment addressing the role of prevalence rather than intensity is required to substantiate this hypothesis. Based on the final frequency distribution generated for 1996, the removal of 45% of the worm population from lightly infected hosts (the left side of the frequency distribution; see Fig. 1) would decrease the prevalence of *H. occidua* from 55.3% to 7.1%. Using the closed model population estimate of the number of frogs present in Charlie's Pond in 1996 (84 frogs), this would amount to reducing the number of infected frogs from 46 to 6. In terms of dispersal of infected feces, this should amount to a reduction of approximately 85%.

Although temporally complex, localized transmission of *H. occidua* in this system makes the life cycle spatially simple. The probability of a frog becoming colonized is dictated by its location in the pond, i.e., whether it resides in an area previously occupied by an infected frog (Zelmer et al., 1999). This is analogous to the infection probabilities generated by the direct life cycles of certain human parasites. The relatively immobile infective stages of human ascarids, hookworms, and whipworms suggests that transmission in these systems also might be driven by the distribution of infective packets rather than the absolute number of infective stages.

#### Implications for selective treatment

The 3 possible explanations for the stability of the *H. occidua* host-parasite system in Charlie's Pond, i.e., inefficient treatment, reservoirs of infection, prevalence-based transmission, and their potential interactions are not unique to this system. In fact, they are all reasonable interpretations of the lack of success that has been demonstrated for selective treatment (Asaolu et al., 1991). In addition to a lack of consideration of prevalence-based transmission, selective protocols for treatment of human helminthiasis are based, in part, on a faulty assumption. The suggestion that selective treatment will have a substantive impact on the net production of transmission stages (Anderson and Medley, 1985; Medley, 1994) is only true at the individual host level. At the host population level, lower abundance classes contribute the majority of both infective stages and infective packets released into the environment. Figure 6A depicts Anderson and Medley's (1985) fit of Croll et al.'s (1982) data describing the relationship between fecundity and intensity in *Ascaris lumbricoides*. The secondary y-axis represents total egg output per individual as the result of this relationship, assuming a 1:1 sex ratio for *A. lumbricoides* (Delgado y Garnica and Martinez-Murray, 1970; Mello, 1974; Arfaa and Ghadrian, 1977; Croll et al., 1982). At the individual host level, egg production is positively associated with infection intensity. At the level of the host population, however, egg production weighted by the proportion of individuals in each abundance class (calculated from Croll et al.'s [1982] reported mean and *k* for each age class and averaged over all age classes) clearly demonstrates that the lower abundance classes (which are not targeted by selective treatments) are responsible for most of the environmental contamination with infective stages (Fig. 6B). Thus,

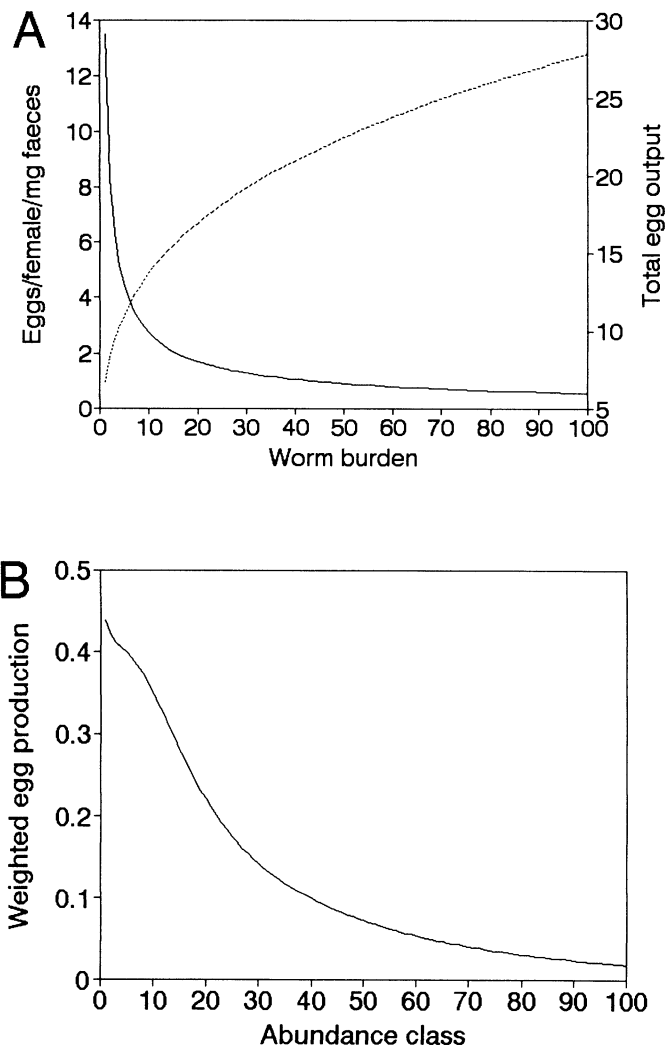


FIGURE 6. Egg output in a human population infected with *Ascaris lumbricoides* (data from Croll et al. [1982]). (A) Effect of intensity on egg production by female worms (solid line) and total egg output by individuals as a function of worm burden (dashed line). (B) Population-level weighted egg production by infection class.

any success of selective treatment in reducing intensity-dependent morbidity will be the direct result of worm removal, rather than a decrease in further recruitment within the population. This control measure, therefore, should be considered as an individual, rather than a population-level treatment, because it only alleviates morbidity by treatment of disease.

Aggregation of infections dictates that, because of their greater numbers, lightly infected individuals will be the greatest dispersers of infective packets, contributing enormously to the probability of other members of the population coming into contact with infective stages. The dynamic nature of *A. lumbricoides* infection demonstrated by Peng et al. (1998) suggests that heavy infections result from repeated exposure rather than from a single, heavy infective dose. Thus, heavy intensity and, therefore, morbidity are also products of the number of infective packets in the environment, i.e., a function of infection prevalence, not intensity.

Although the present investigation cannot isolate a single

cause for the lack of response to worm removal in Charlie's Pond, it does support empirical evidence from treatment of human helminths that suggests disruption of transmission cannot be accomplished through selective treatment (Bundy et al., 1990; Asaolu et al., 1991). Although it has been argued that mass treatment is a financially inefficient means of distributing control measures, the fact that selective treatments must be continuous in order to maintain low levels of intensity has never been factored into the cost equation. Moreover, recent empirical work on treatment of *A. lumbricoides* with levamisole demonstrated that even the short-term costs (both per person and per 1,000 eggs per g feces reduction in intensity) are greater for selective treatment than for targeted or mass treatment (which was the most cost efficient) because of the costs associated with identifying heavily infected individuals (Holland et al., 1996). Although data on a single parasite from 1 locality cannot be expected to have universal applicability, we would suggest that treatment protocols aimed at disrupting helminth transmission based on theoretical models might benefit from a re-evaluation that considers distribution of infective stages as the result of infection prevalence.

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