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Variation in fecundity among populations of snails is predicted by prevalence of castrating parasites

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ABSTRACT

Life-history theory predicts that high mortality should cause selection for high reproductive effort. Because parasitic castration has an equivalent role to mortality, from a fitness perspective, populations with high prevalence of castrating parasites are predicted to exhibit high reproductive effort relative to populations with low prevalence. I examined this prediction by studying populations of the freshwater snail, *Elimia livescens*, that vary in prevalence of castrating trematodes. Specifically, I determined whether there was a positive relationship between reproductive output and prevalence of castrating trematodes among populations. Consistent with predictions, females from populations with a high prevalence of castrating trematodes produced more eggs than females from populations with a low prevalence. Either genetic canalization or phenotypic plasticity may have caused the relationship between reproductive output and parasitism. By either mechanism, the results suggest that castrating parasites shape the life histories of their hosts.

Keywords: castrating parasites, fecundity compensation, life-history theory, reproduction, snails, trematodes.

INTRODUCTION

Life-history theory predicts selection for increased reproductive effort in populations with high extrinsic mortality (Kozlowski and Uchmanski, 1987). Parasites that castrate both sexes of infected hosts have an equivalent role, in an evolutionary context, to mortality, since the host cannot contribute additional offspring to the next generation. Thus, castrating parasites should cause selection for increased reproductive effort in populations with high parasitism, relative to populations with low parasitism (Forbes, 1993). Depending on the nature of selection, variation among individuals in reproductive output can be genetically canalized, or can be the result of a labile response to environmental conditions (i.e. phenotypic plasticity: Lively, 1986; Harvell, 1990). Consequently, differences among populations exposed to varying levels of parasite-imposed selection may be based on individuals possessing developmentally labile or canalized traits. Whether based on genetically canalized traits or phenotypically plastic responses, allocation to reproduction should be

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positively associated with prevalence (frequency of parasitized individuals) of castrating parasites among populations of hosts. I examined this prediction among populations of a freshwater snail, *Elimia livescens* (formerly *Goniobasis livescens* [Menke]), which vary in prevalence of castrating trematodes. Specifically, I determined whether unparasitized individuals in populations with a high prevalence of castrating trematodes invested more in reproduction than unparasitized individuals from populations with a low prevalence of castrating trematodes.

Effects of parasitism on host reproduction have been reported elsewhere (Minchella and Loverde, 1981; Thornhill *et al.*, 1986; Schallig *et al.*, 1991; Sorci *et al.*, 1996; but see Schrag and Rollinson, 1994, for a counter-example). Most of these studies demonstrated that parasites affect reproductive effort of laboratory-reared animals that were experimentally exposed to parasites (Minchella and Loverde, 1981; Thornhill *et al.*, 1986; Schallig *et al.*, 1991; Schrag and Rollinson, 1994). In contrast, in the present study I compared reproduction among populations in natural conditions.

MATERIALS AND METHODS

Elimia livescens (Prosobranchia: Pleuroceridae) is a freshwater snail that inhabits permanent streams, rivers and large lakes in the eastern United States, north of Kentucky. These snails are dioecious, oviparous (Jewell, 1931), iteroparous (Dazo, 1965) and breed seasonally, primarily in April and May (Jewell, 1931; Dazo, 1965). *Elimia livescens* is a first intermediate host to over a dozen species of trematodes; vertebrates are the definitive host. Most of these parasites castrate both sexes of the snail (A. Krist, unpublished data). Host castration can occur directly by the parasite consuming the gonad, or indirectly by the parasite withdrawing nutrients or altering hormones (Baudoin, 1975). The proportion of snails that are parasitized by castrating trematodes is highly variable among stream populations of *E. livescens* in southern Indiana (Table 1).

I measured prevalence as the number of hosts infected with one or more type of castrating trematode (Bush *et al.*, 1997). Because castration causes reproductive ‘mortality’, prevalence of castrating trematodes is an estimate of the selection pressure applied by trematodes within populations (Lafferty, 1993). I estimated prevalence by calculating the geometric mean of prevalence in multiple years in seven populations, and in one population I based my estimate on data from one year only (see Table 1). I used the geometric mean of several years to estimate prevalence because, in these long-lived snails, the response to selection in different populations should reflect the mean selection pressure over many years (severe in years with high prevalence, relaxed in years with low prevalence). I calculated a size-corrected estimate of prevalence because large individuals are more frequently infected than small individuals (Krist, 1998). Also, the size-corrected prevalence more accurately reflects the threat of infection because snail length is correlated with age. Thus, for each population in each year, I calculated prevalence from the subset of individuals whose lengths fell between the smallest infected and the largest uninfected snail (in the range where the size frequency distributions of uninfected and infected snails overlapped). Within this subset, the threat of infection for uninfected snails is real; conspecifics in the same size and age range are infected.

I collected snails from each of eight populations in Indiana approximately every 32 days, from mid-April to mid-July 1996. Although the peak egg-laying period for *E. livescens* is reported to be April and May (Jewell, 1931; Dazo, 1965), I also sampled in June and

Table 1. Prevalence of castrating trematodes in the eight populations of *Elimia livescens* that were examined in this study

Population	Prevalence 1993	Prevalence 1994	Prevalence 1996	Geometric mean	Sample size
Clear Creek	0.51	0.48	0.07	0.26	512
Crane	0.12	0.05	0.12	0.09	201
Goose Creek	0.17	0.14	0.05	0.11	463
Indian Creek	0.02	0.16	0.12	0.07	230
Judan Branch	0.05	0.00	0.00	0.00	25*
McCormick's Creek	—	—	0.13	0.13	102
Stout Creek	0.03	0.04	0.02	0.03	415
Twin Lakes Creek	—	0.35	0.22	0.28	271

Note: In McCormick's Creek, prevalence was surveyed only in 1996 because a severe population crash occurred at the original sampling site and, consequently, in 1996, I collected snails for measurement of prevalence and reproductive effort several kilometres from the previous site. For each population and each year, prevalence was estimated from the subset of snails whose lengths fell within the region of overlap between the size frequency distributions of uninfected and infected snails (greater than the smallest infected snail and less than the largest uninfected snail). Geometric mean refers to the geometric mean of prevalence for the years that were surveyed. Sample size refers to the number of snails used to calculate the geometric mean of prevalence. Populations are separated by at least 8 km overland and a much greater distance along water courses.

* For Judan Branch, only 4 of the 374 snails examined were parasitized. The size criteria for inclusion meant that the sample size was reduced significantly, but the estimate of prevalence is robust.

July because I had previously observed females laying eggs in June and I wanted to be certain that sampling occurred over the entire reproductive period for each population. Sampling began in April because, prior to this month, the snails are burrowed into the substrate of the stream to escape winter temperatures. The data were pooled for the entire 4-month period because populations reproduced at different times and comparisons of reproduction among populations were of interest, regardless of the timing of reproduction. For each sample, I collected approximately 20 unparasitized females for measurement of reproductive effort.

I measured allocation to reproduction in females by counting the number of eggs laid in a 5-day period. In preliminary studies, snails readily laid eggs within a few hours of bringing them into the laboratory. After 24 h acclimatization, I placed females individually into plastic cups (205 ml of water) in which the water was aerated and replaced daily. After 5 days, I counted the number of eggs that had been laid in each cup. Because the mass of individual eggs did not differ among populations (one-way analysis of variance comparing the mass of individual eggs from five populations; $F_{4,48} = 0.41$, $P = 0.804$), egg counts reflect reproductive output. Therefore, differences among populations in reproductive allocation should be detected by differences in egg number.

I also measured the length of the shell and dissected the adult snail to determine whether it was parasitized. Parasitized females were excluded from the study. Although increased reproductive output can occur in recently parasitized snails that have not yet been castrated (Minchella and Loverde, 1981; Thornhill *et al.*, 1986), all infected individuals were excluded because I was not able to determine how recently infections were acquired. For every month, each population was represented by 16–20 uninfected snails. For the entire study, each population was represented by 73–80 uninfected snails.

I used linear regression to assess the relationship between reproductive output and prevalence of parasites in each population. The dependent variable was the mean number of eggs produced by the reproductive females in each population combined over all months (8 points; this variable was log-transformed to produce homogeneous variances). The number of eggs was adjusted for length of the snail (using the adjusted means calculated from individual fecundity and length in an analysis of covariance; Norusis, 1994) because the number of eggs produced by each snail was positively related to the length of the snail ($F = 3.55$, d.f. = 6, $P = 0.061$). The independent variable was the size-corrected, geometric mean prevalence of castrating parasites for each population (as described above).

RESULTS

Linear regression analyses revealed that the number of eggs produced by reproductive females was positively and significantly related to the geometric mean prevalence of castrating trematodes ($r^2 = 0.66$, regression coefficient = 2.53, $P = 0.014$, d.f. = 1) (Fig. 1). Very similar results were obtained when the arithmetic mean of prevalences was used instead. Consistent with previous studies (Jewell, 1931; Dazo, 1965), most of the snails laid eggs in April and May. In contrast, few snails reproduced in June or July; no females laid eggs in four populations and in three populations there were, at most, two females who reproduced. This major decrease in reproduction in the later months of the study suggests that the sampling period was representative of the entire reproductive period for these populations.

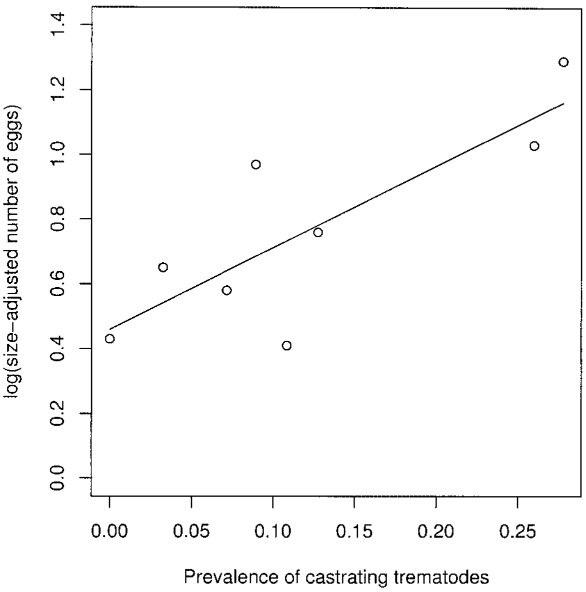

Fig. 1. Each point represents the log-transformed value of the size-adjusted mean number of eggs and the geometric mean prevalence of castrating trematodes. The mean number of eggs was obtained by pooling values of 4–40 uninfected females over four sampling dates from April to July 1996. See Table 1 for information about mean prevalence. The regression is significant ($P = 0.014$).

DISCUSSION

Life-history theory predicts high optima for reproductive effort in populations with high prevalences of castrating trematodes. The results of this study are consistent with this theoretical prediction; the number of eggs produced by uninfected females was greater in populations with a high prevalence of castrating trematodes than in populations with a low prevalence.

Differences among populations exposed to varying levels of parasite-imposed selection may be based on individuals possessing phenotypically plastic or canalized traits. The nature of selection should determine whether invariant or phenotypically plastic reproductive strategies are favoured. Phenotypic plasticity is expected to evolve when the threat of parasitism is variable in space or time, reliable cues indicate the threat of parasitism, and relatively high costs are associated with possessing high reproductive effort when parasite prevalence is low (Lively, 1986; Harvell, 1990; Michalakis and Hochberg, 1994). Conversely, invariant reproductive output should be favoured when selection pressure by parasites is constant, when no reliable cues exist, and when the costs of suboptimal reproductive allocation are relatively low (Lively, 1986; Harvell, 1990; Michalakis and Hochberg, 1994).

In hosts, both phenotypically plastic and genetically invariant traits have been produced through selection by parasites. For example, phenotypic plasticity causes increases in reproductive allocation in response to the threat of parasitism (Minchella and Loverde, 1981; Minchella, 1985; Thornhill *et al.*, 1986). This phenomenon, known as fecundity compensation, ensures hosts some reproduction when a threat of parasitic castration exists. Thus, fecundity compensation can be viewed as a host defence by reducing the parasite's effect on the host (Minchella and Loverde, 1981; Minchella, 1985; Forbes, 1993). In this study, fecundity compensation could explain differences among populations in reproductive output because an individual's likelihood of exposure to parasitism should be positively related to the prevalence of a population. Parasitism may also cause selection for genetically canalized traits. For example, parasitism is negatively correlated with size at first reproduction in salt marsh snails and reciprocal transplant experiments have shown that variance in size at first reproduction has both environmental and genetic components (Lafferty, 1993). Differences in reproductive output among populations of *E. livescens* may also have a genetic component. Genetic differentiation among populations is possible because gene flow among the stream populations is expected to be very low; stream populations of *E. proxima* separated by similar distances to those found in this study have been shown to exhibit very little gene flow (Dillon, 1984). Although the results of this study suggest that parasitism underlies differences among populations in reproductive output, they cannot distinguish between phenotypic plasticity and genetic canalization as the mechanism for these differences. An experiment in which females from different populations that had not been exposed to parasites were reared in a common environment or in a reciprocal transplant design might reveal the underlying mechanism.

As with all correlational studies, it is possible that the relationship between prevalence and reproductive output was not caused by parasites but was caused by another characteristic of populations that covaries with prevalence or reproduction. For example, if some correlate of low fecundity, such as poor food quality or low food availability, also causes low prevalence, then a positive relationship between prevalence and reproductive investment should occur. Also, if parasitic castration reduces the density of snails in populations with high prevalence, then reduced competition for resources could increase the energy available for reproduction and, consequently, produce a relationship between high fecundity and high prevalence. These hypotheses merit direct experimentation. However, the result reported here is not simply a correlation. A positive relationship between reproductive effort and parasite prevalence is a critical prediction of theory and, consequently, the among-population comparison is a test of theory.

Although the results are predicted by theory, the detection of the relationship between prevalence and fecundity could have been obscured by factors that are not controlled in field studies. For example, the study examined only eight populations, which probably differed in a variety of biotic (e.g. competitors, predators) and abiotic (e.g. temperature, size of the stream, substrate) attributes. Therefore, if the relationship between reproductive investment and prevalence is caused by parasitism, its detection may suggest that parasitism has a powerful effect on populations.

In conclusion, consistent with life-history theory, females from populations with a high prevalence of castrating trematodes have higher fecundity than females from populations with a low prevalence. Although differences in reproductive output among populations may be based on canalized or phenotypically plastic traits, either mechanism suggests that castrating trematodes affect reproductive output in populations of *E. livescens*. In combination with the results of previous studies of other host–parasite systems (Minchella and Loverde, 1981; Thornhill *et al.*, 1986; Schallig *et al.*, 1991; Lafferty, 1993; Jokela and Lively, 1995; Sorci *et al.*, 1996), the present findings suggest that parasites have important effects on the life histories of their hosts.

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