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The marine snail, Cerithidea californica, matures at smaller sizes where parasitism is high

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I investigated life-history and parasitism in the salt marsh snail, *Cerithidea californica*. Latitude and growing conditions were important factors determining maturation size. After accounting for environmental variation, there was a negative association between the maturation size of snails and the prevalence of parasitic castration by larval trematodes. As predicted by life-history theory, this may represent an adaptation against parasitism that is similar to previous observations of life-history adaptations in species subject to predation or disturbance. However, it was unclear whether this adaptation was due to phenotypic plasticity or genetic differences among populations resulting from natural selection so I conducted a reciprocal transplant between sites with high and low prevalence and found source population differences in maturation size. It appears, therefore, that the life-history differences between these populations are at least partially genetic or may represent an adaptive developmental switch that was initiated prior to the transplant.

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A parasitic castrator eliminates the future reproduction of its host. In this sense, being castrated by a parasite is much the same as being eaten by a predator (Kuris 1974). Parasitic castration is common among gastropod, crustacean and echinoderm hosts and occurs, but is less common, among plants, helminths, cnidarians, annelids, insects and vertebrates. In some cases, prevalence (the proportion of hosts parasitized, Margolis et al. 1982) is high, leading to substantial reductions in the reproductive output of the host population (Kuris 1974, Brown et al. 1988, Lafferty 1991, Kuris and Lafferty 1992). For these reasons, it is possible that parasitic castrators may be a strong selective force acting on many host species. Clearly, hosts have evolved defenses against pathogenic parasites (e.g., Anderson and May 1982). With behavioral, physiological, and morphological adaptations, hosts can avoid infection, minimize pathology or kill parasites. Alternatively, hosts can increase the chance that they will reproduce before castration by adjusting their life-history strategies (Minchella 1985, Thornhill et al. 1986).

Much of the work done on parasitic castration has been with snails and larval trematodes. Asexual reproduction of larval trematodes within the snail nearly always leads to complete castration of that host from a single infection (Kuris 1973). For at least one species of snail, *Biomphalaria glabrata,* there is an attempt to compensate for the effects of castration; infection with a larval trematode, *Schistosoma mansoni,* results in a sudden burst of reproductive effort before castration occurs (Minchella and Lo Verde 1981, Thornhill et al. 1986). In this case, infection cues the snail to its limited reproductive future and it is able to act accordingly. The risk of parasitism might also affect the life-history strategy of unparasitized snails. If natural selection influences life-history parameters, then unparasitized snails should mature earlier in populations that have a high prevalence of trematodes than in populations with a low prevalence of trematodes (Keymer and Read 1992).

The optimal age at maturity is a trade off between present reproductive activity and the probability of future reproduction (Stearns 1989). These are, in turn, subject to the ways that size and age relate to fecundity and survivorship (Pianka 1976). There are likely to be

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costs associated with early maturation, such as a lower reproductive potential if maturation reduces future reproductive success (reviewed in Stearns 1989; Schultz and Warner 1989). Furthermore, if fecundity increases with size, future reproductive success increases as the individual allocates more time and energy to growth (Bagenal 1978). Reproducing early, however, has the twofold advantage of decreasing generation time and increasing the probability that the individual will survive to maturity (Cole 1954, Lack 1954, Williams 1966). The lower the prospects for survival, the more likely it is that gains in reproductive time will offset costs of early maturation such as reduced growth. Therefore, in the presence of a parasitic castrator, hosts that delay maturation could have shorter reproductive lives and reduced fitness. Although this has not been shown for hosts subjected to parasitism, high rates of predation and disturbance have been shown to select for early maturation (Tinkle and Ballinger 1972, Solbrig and Simpson 1974, Law et al. 1977, Reznick and Endler 1982, Reznick 1990).

In some cases, the relationship between mortality and maturation has been shown to be dependent on the relative susceptibility of different age or size classes. If immature hosts are immune, there can be selection to delay maturity (Barcaly and Gregory 1982). Likewise, if large individuals are immune, there can be selection for increased growth at the expense of present reproductive effort (Crowl and Covich 1990). For this reason, the general prediction of early maturation as a response to parasitism may not be valid if immunity varies with size or age.

To examine associations between parasitic castration and life-history parameters, I investigated geographic variation in the prevalence of parasitic castration by larval trematodes and the size at which snails developed discernible gonads. For this, I chose isolated populations of the horn snail, *Cerithidea californica* (and its southern congener, *C. mazatlanica*). These snails are parasitized by many larval trematode species that, as adults, are primarily parasites of shore birds (Martin 1972). Prevalence is variable among marshes but commonly reaches levels where over half of the adult population is castrated (Lafferty 1991). Because trematodes parasitically castrate mature and immature individuals of both sexes (Lafferty 1991), and infections appear to be permanent (Sousa 1983), I predicted that snails should mature earlier in populations with high rates of parasitism.

Early maturation as an adaptation to the risk of parasitic castration could be based on phenotypic plasticity or represent an increase in the frequency of early maturing genotypes. If life-history is plastic, individuals may base the timing of maturation on cues they receive from the immediate environment. If the age of maturation is genetically determined, however, snails from different populations should maintain some differences in their life-history when reared under identical conditions. To investigate this second prediction, I reciprocally transplanted snails from areas with a high and low prevalence of parasitism. This experiment was limited to a within generation experiment because it was not possible to raise these snails in the laboratory.

As predicted, there was a negative association between the prevalence of parasitic castrators and maturation size within a salt marsh and among salt marshes. In addition, snails from a population with high prevalence and a population with low prevalence maintained significant differences in maturation size after the reciprocal transplant.

Materials and methods

General procedures

The estimations of snail density and mean size at each site involved placing a transect line across a tidal channel. Beginning at the upper vegetated margin of the bank, I placed adjoining 700 cm^2 circular "quadrats" along the transect to the center of the channel (or to the lower limit of the distribution of snails). The number and lengths of the snails in each quadrat were then recorded. I placed two extra quadrats, one on each side of the quadrat with the highest density, at a distance of one meter perpendicular to the transect line. Snails from these additional quadrats, as well as from the quadrat with the highest density, were used to characterize snail population density and size distribution. These estimates did not include all quadrats because snail density varies with intertidal height (Page and Lafferty 1993). Since salt marsh channels vary in width and bank slope, sampling from the region of the quadrat with the highest density insured that snail densities were representative of the vertical zone that snails appeared to prefer. Finally, because the nature of the sediment might indicate habitat quality for salt marsh animals (Reise 1985), I scored the sediment at each site according to its coarseness (Lafferty 1991).

To determine infection and maturation status, I dissected additional snails (sample sizes indicated below) and, with a dissecting microscope, assayed them for the presence of larval trematodes or a visible gonad (trematode rediae or sporocysts usually displace the gonad and digestive gland region that occupies the posterior third of the spire). Male snails were identifiable by the presence of a yellow gonad, mature females by the presence of a green gonad, and immature individuals by the absence of gonadal material that usually covers the brown colored digestive gland (Bright 1960). An infection with larval trematodes obscures gonad color and maturation status. Using these data, I estimated the prevalence of parasitic castrators and maturation size for each sample of snails.

Measuring the prevalence of parasitism provided an estimate of the selective pressure from trematodes in a

population. The prevalence of infection increases with snail size (possibly because older, larger snails have had a longer exposure to infection (Sousa 1983)). Because variation in snail size among populations could influence prevalence, it was necessary to standardize samples to a single size class. Therefore, I calculated the prevalence of parasitic castrators in a host population based on the proportion of snails parasitized in a sample of one hundred 20–25 mm snails. Snails in this size class were common in all the populations.

I could not determine the age of maturity for these snails. However, as size is likely to be a function of age, size at maturity provides an alternative measure. For instance, Brown (1985) found that freshwater snails that matured at an early age also matured at a small size. Therefore, I determined the average size at which gonads were visible. The presence of visible gonads does not indicate maturity in the absolute sense. For this reason, "maturation size" is a measurement of the size at which the snail directs energy toward reproduction. Only unparasitized snails were used since "maturation" cannot be determined in castrated snails. Excluding parasitized snails from the maturation estimate did not bias the results in favor of the prediction of a negative correlation between prevalence and maturation size (Lafferty 1991).

Each sample consisted of approximately two hundred 10–25 mm snails grouped into 1 mm size classes. I collected larger numbers of snails from sites with high prevalence to insure similar sample sizes of unparasitized snails among populations (the minimum number of unparasitized snails used in each 1 mm size class was 10). A weighted least squares regression of the percent of mature snails in each size class indicated the relationship between size and maturation. Although the relationship between gonadal development and size is probably sigmoid (Wenner 1972), a bounded linear approximation provided a good fit (mean $R^2 = 0.84$). Setting the lower bound at the largest size class in which ten of ten snails were immature and the upper bound at the smallest size class in which ten of ten snails were mature constrained the regression to the nearly linear portion of the curve. The regression provided an estimate of the size at which half of the unparasitized snails had discernible gonads. Using the midpoint of this regression minimizes the potential error of the estimate. Therefore, I estimated maturation size as the snail size for which one half of the snails had visible gonads.

Variation within and among populations

Maturation size and prevalence of parasitic castrators were estimated from eight sites within Carpinteria Salt Marsh. Using a map of the marsh, I marked channel sites at roughly 50 m intervals that were within a 100 m distance from a main access road and had banks stable enough to walk on. Eight of these sites were then chosen at random for the survey.

I determined growing conditions for each site over a three month period. Snails were collected from different sites, mixed, numbered, and kept at each site in 700 cm^2 open-topped mesh cages for three months. Snails used in this comparison were unparasitized and from similar size classes. I measured the change in length of each snail monthly and used the growth rates of uninfected snails (55 snails for each of the eight sites) to characterize the "growing conditions" at a site (see Lafferty 1991 for details of the design).

Maturation size and prevalence of parasitic castrators were estimated from seventeen other salt marshes in California (USA) and Baja California (Mexico). A series of berms and flood control pipes isolated the two Bolsa Chica populations; stretches of open coastline isolated all other populations. Dates and detailed locations are in Lafferty (1991). At each location, I sampled from tidal channels, or, if these were not available, from marsh pans (unvegetated depressions in the pickleweed) or tidal flats. Usually, samples were collected within a 100 m radius of a randomly chosen accessible area. This limited the impact of walking on the soft surface sediments, the pickleweed beds, and the snail populations.

Multiple regression analysis, with maturation size as the dependent variable, was used to determine whether the data from Carpinteria Salt Marsh supported the prediction of a negative association between maturation size and prevalence of parasitic castrators. Prevalence and a composite variable were the independent variables. I used a composite variable because the small number of sites (8) limited the inclusion of a large number of independent variables. The composite variable was equal to my estimate of the growing conditions at a site divided by the product of the density of snails and the square of the mean snail size. This combination of variables had biological meaning as it indicated the per-capita food availability at a site (weighted by snail mass). This approach was supported by a similar analysis that used each of the three contributing variables as separate independent variables. The inclusion of sediment grain size in the composite variable had no effect on the results of the analysis. I have reported all probabilities based on a two tailed prediction unless otherwise stated.

Multiple regression analysis, with maturation size as the dependent variable, helped to determine whether the data among salt marshes supported the prediction described above. The larger number of replicates (18 sites) made it feasible to enter prevalence, snail density, mean snail size, sediment grain size, and latitude as independent variables. By averaging the data from the eight sites in Carpinteria, it was possible to include Carpinteria as a single site in this analysis.

Along with these statistical analyses, I plotted the residuals of prevalence against the residuals of matura-

Table 1. The data that were obtained for *Cerithidea californica* in Carpinteria Salt Marsh are expressed as follows. Maturation size (Mat) is the size, in mm, at which 50% of snails have discernible gonads. Prevalence is the proportion of 100, 20–25 mm snails (Prev 20) or all snails (Prev All) that were infected. Density (Dens) is the mean number of snails in a 700 cm^2 circular "quadrat" (three quadrats total). Size is the mean snail length, in mm (three quadrats total). Growing condition (Grow) is an experimentally determined rate of growth in mm/month. Sediment type (Sed) is a score from 1–4 that increases with grain size. Sampling dates are month.day, 1991.

Carpinteria Salt Marsh	Mat	Prev 20	Prev All	Dens	Size	Grow	Sed	Date
Site 1	16.2	0.54	0.52	42.0	22.1	1.25	2.15	11.9
Site 2	15.8	0.58	0.77	8.7	27.6	1.45	2.12	11.11
Site 3	15.5	0.53	0.83	11.7	29.6	1.54	2.62	10.6
Site 4	16.1	0.62	0.84	17.0	27.0	1.19	2.85	10.2
Site 5	16.7	0.37	0.96	16.3	29.2	1.38	2.28	10.30
Site 6	17.5	0.33	0.25	41.0	22.0	1.44	2.44	10.27
Site 7	18.1	0.61	0.50	5.3	27.1	1.45	1.65	11.2
Site 8	17.6	0.58	0.86	7.3	27.4	1.83	2.49	11.1

tion size (these residuals were obtained by separately regressing prevalence and maturation against the other independent variables). This yielded a graphical representation of the association between prevalence and maturation size without the effects of the other independent variables.

Environmental and genetic effects

To test for genetic differences in maturation size, I conducted a reciprocal transplant experiment between two Southern Californian salt marshes. I collected five hundred and fifty snails from a population with a high prevalence of parasitic castrators (Carpinteria Salt Marsh; 52% prevalence among 20–25 mm snails, n = 800) and six hundred and sixty snails from a population with a near zero prevalence of parasitic castrators (Bolsa Chica State Beach parking lot, 0% prevalence among 20–25 mm snails, n = 250). Snails were collected over a wide area to ensure that each snail was representative of its source population. These snails were at least 5 mm in length (so that they could be marked with epoxy paint) but at least 2 mm smaller than the smallest mature individuals. Marked snails were transplanted back to their own population (as a control) or to the novel (reciprocal) habitat. The transplants occurred in April before the egg-laying season. The possibility of genetic differences in maturation between populations

Table 2. The data that were obtained for *Cerithidea californica* and *C. mazatlanica** are expressed as follows. Latitude (Lat) is in degrees. Maturation size (Mat) is the size, in mm, at which 50% of snails have discernible gonads. Prevalence is the proportion of 100, 20–25 mm snails (Prev 20) or all snails (Prev All) that are infected. Density (Dens) is the mean number of snails in a 700 cm^2 circular quadrat (three quadrats total). Size is the mean snail length, in mm (three quadrats total). Sediment type (Sed) is a score from 1–4 that increases with grain size. Sampling dates are month.day, 1991. A map of all locations is in Lafferty (1991).

Site	Lat	Mat	Prev 20	Prev All	Dens	Size	Sed	Date
Drake's Estero	38.1	16.1	0.15	0.09	39.0	23.3	2.20	10.18
Palo Alto (S. F. Bay)	37.5	18.4	0.01	0.00	34.0	16.5		10.20
Morro Bay	35.3	18.4	0.42	0.19	19.3	14.2	2.06	10.21
Goleta Slough	34.4	19.8	0.19	0.19	35.6	21.3	1.53	10.16
Carpinteria Salt Marsh	34.4	16.7	0.52	0.69	18.7	26.5	2.40	table 1
Venice Canals	34.0	16.5	0.34	0.25	44.3	18.9	3.11	10.10
Anaheim Bay	33.8	19.2	0.33	0.27	18.7	26.1	2.32	10.10
Bolsa Chica Parking Lot	33.7	19.8	0.01	0.02	18.7	26.6	2.92	10.9
Bolsa Chica Slough	33.7	17.6	0.25	0.31	13.7	25.1	3.08	10.9
Newport Back Bay	33.6	18.2	0.11	0.32	6.3	24.5	1.94	10.8
Mission Bay	32.8	16.8	0.54	0.52	60.7	21.2	1.92	9.24
Tijuana Slough	32.5	17.3	0.89	0.95	13.6	25.5	1.25	9.24
Estero de Ensenada	31.8	16.4	0.41	0.41	31.0	18.1	2.89	9.23
Bahia San Quintín	30.5	19.8	0.21	0.25	43.0	22.4		9.22
Bahia Las Animas*	28.8	18.5	0.00	0.06	5.7	22.7	3.42	9.20
Laguna Ojo de Liebre*	28.0	22.4	0.10	0.15	66.7	20.2	2.94	9.15
Estero el Coyote*	26.8	19.9	0.04	0.06	10.3	18.4	2.55	9.18
Estero la Bocana*	26.8	19.8	0.64	0.62	102.5	22.0		9.17

Table 3. Multiple regression analysis for 8 sites within Carpinteria Salt Marsh with maturation size as the dependent variable. Grow/mass is a composite variable that is equal to the growing conditions at a site divided by the product of the density of snails and the square of the mean snail size. Squared multiple R = 0.682.

Ind. var.	Std. Coef.	T	p (2 tail)
Constant	0.000	6.798	0.000
Prevalence	−0.645	−2.183	0.081
Grow/mass	0.952	3.221	0.023

Table 4. Multiple regression analysis for 18 salt marshes with maturation size as the dependent variable. Squared multiple R = 0.628.

Ind. Var.	Std. Coef.	T	p (2 tail)
Constant	0.000	6.798	0.000
Prevalence	−0.688	−3.133	0.009
Latitude	−0.632	−3.208	0.008
Density	0.260	1.293	0.220
Size	0.074	0.396	0.699
Sediment	−0.412	−1.890	0.083

could be rejected if no differences in maturation size remained following the transplant.

I collected each group of transplanted snails before all had matured because the trait of interest was the proportion of individuals with discernible gonads. Although multiple generation studies might have been able to eventually reject the role of early phenotypic plasticity, it would not have been practical to intersperse treatments and follow these long lived snails for more than a single generation. After 83 d, I recovered as many snails as possible (37%), then dissected and checked them for visible gonads. Groups were compared to determine whether the snails from the two populations still differed in maturation size after being raised in the same environment (as predicted by the genetic difference hypothesis). I considered snails as replicates since I had interspersed transplanted snails with control snails and each snail was a random representative of its habitat. Cochran's method was used to compare the maturation size of the four treatments (Everitt 1977).

Results

Association between parasitism and maturation

The results were consistent with the prediction of early maturation in areas with high amounts of parasitism. Tables 1 and 2 present the data gathered at all sites. Within Carpinteria Salt Marsh, there was a negative standardized partial regression coefficient for prevalence and maturation size (Table 3). This association was significant at the one tailed level ($p = 0.04$). The plot of the residuals of maturation size and prevalence illustrates how prevalence accounts for much of the unexplained variance in maturation size (Fig. 1). There was a significant effect of the composite variable (grow/mass) on maturation size ($p = 0.023$) The standardized coefficient for this association indicated that in areas where growing conditions were good, snails matured at larger sizes. This suggests a strong environmental component to maturation size associated with resource availability.

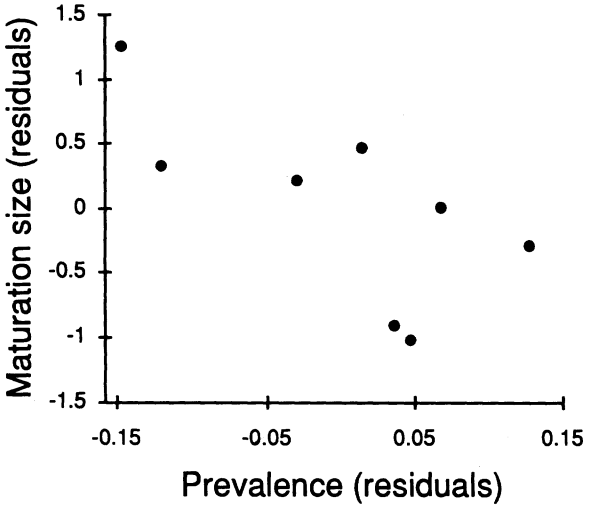

Fig. 1. A scatterplot of the residuals of maturation size and prevalence of trematodes (see Table 3) for 8 sites within Carpinteria Salt Marsh Reserve.

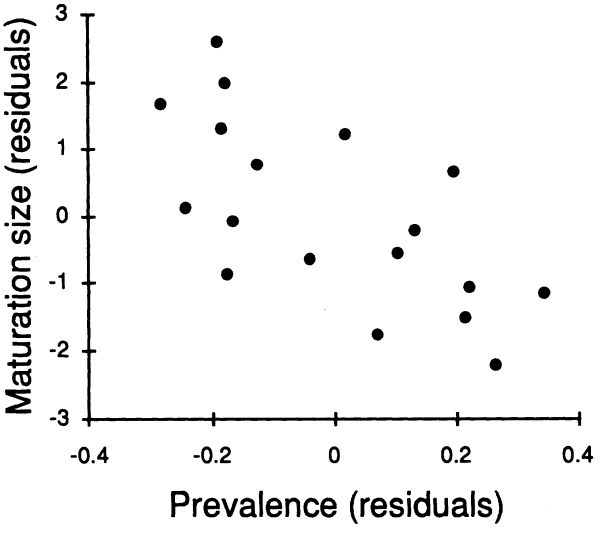

Fig. 2. As in Fig. 1, a scatterplot of the residuals of maturation size and prevalence of trematodes (see Table 4) estimated for 18 populations of *Cerithidea californica* and *C. mazatlanica* along the California and Baja California coasts.

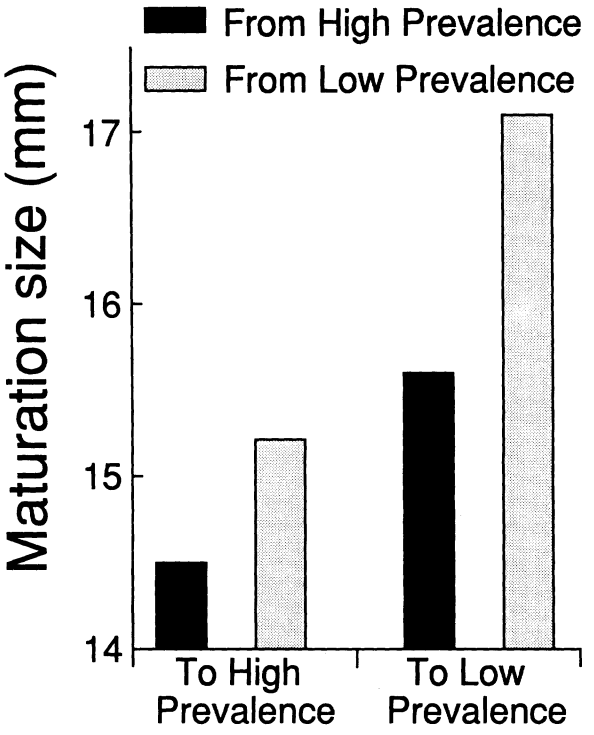

Fig. 3. Estimated size at which 50% of snails were mature after a reciprocal transplant between Carpinteria Salt Marsh (high prevalence) and Bolsa Chica parking lot (low prevalence) (448 snails total). Values presented in this figure were estimated for illustrative purposes using least squares regression and for this reason do not include the error of the estimate. Cochran's method indicated significant differences between groups (see results).

A similar result appeared among populations (Table 4). After other variables were accounted for, there was a negative association between the prevalence of parasitic castrators and maturation size ($p = 0.005$, one tailed). Again, the plot of the residuals illustrates that prevalence accounts for most of the unexplained variance in maturation size (Fig. 2). Latitude also explained much of the variance in maturation size, further suggesting an important environmental component to maturation size ($p = 0.008$). Prevalence was not correlated with either growing conditions or latitude.

Environmental and genetic effects

The reciprocal-transplant experiment found source-population effects on snail maturation size. Snails from the two populations maintained significant differences in maturation size when placed in either habitat (Fig. 3, Cochran's method, $p < 0.0001$). In addition, the snails transplanted to Carpinteria matured at smaller sizes than snails transplanted to Bolsa Chica (Fig. 3, Cochran's method, $p < 0.0001$), indicating an environmental effect.

Table 5. Correlation coefficients for variables from eight sites in Carpinteria Salt Marsh. (*) = $p < 0.05$.

	Maturation size	Prevalence
Snail density	−0.045	−0.544
Snail size	−0.307	0.280
Sediment coarseness	−0.155	0.452
Growing conditions	0.832*	−0.180

Discussion

Environmental factors related to the productivity of the environment explained most of the variation in the maturation size of snails. The positive association between growing conditions and maturation size could occur if snails mature at a particular age. For example, in productive environments, fast growing snails develop gonads when they are large (Brown 1985). In turn, snails might grow slower in northern latitudes due to decreased day length, radiance or temperature. This could help explain the negative association between maturation size and latitude. Other studies have also found that the productivity of the habitat is an important predictor of snail life-history strategies (Calow 1981, Brown et al. 1985).

Only after accounting for environmental variation were the effects of parasitism on life-history apparent. The negative association between maturation size and the prevalence of parasitic castrators suggests that snails may have adapted to the risk of parasitic castration by maturing earlier. This could occur if snails that mature early have a longer reproductive life than those that mature late. Early maturation might be more adaptive for males than females because males are apparently more susceptible to infection than are females; the larger maturation size of females supports this prediction (Lafferty 1991). In Carpinteria Salt Marsh, the smallest mature male out of 100 hundred uninfected snails was, on average, 4 mm smaller than the smallest mature female (paired t-test, $N = 8$, $p < 0.001$). This sexual dimorphism did not affect the interpretation of the results.

Multiple regression was necessary to help determine whether the prevalence-maturation size association occurred independent of environmental factors. A simple negative correlation between prevalence and maturation size could, in two ways, incorrectly suggest a causal

Table 6. Correlation coefficients for variables from 18 salt marshes. (*) = $p < 0.05$.

	Maturation size	Prevalence
Snail density	0.247	0.274
Snail size	−0.082	0.140
Sediment coarseness	0.112	−0.490
Latitude	−0.559*	−0.037

relationship between parasitism and maturation size if parasitism covaries with environmental factors that effect maturation size. First, fast growth rates could cause snails to mature at large sizes if maturation size occurred at a set age. Fast-growing snails would be young for their size and have had less exposure to infection. This could cause a negative correlation between the prevalence of parasitic castrators and maturation size. Second, if plentiful food resources cause snails to mature earlier and at smaller sizes, a positive correlation between infection rates and resource availability could cause a negative association between maturation size and the prevalence of parasitic castrators. Here, there is no correlation between prevalence and growing conditions or latitude (Tables 5 and 6). Furthermore, in contrast to the second alternative, increased resources do not lead to a small maturation size in this system. On the contrary, as often happens for snails (e.g., Eisenberg 1966, Brown et al. 1985), lowered densities and increases in food resources lead to increased growth rates which led to a larger maturation size in the present study (Lafferty 1991). Nonetheless, as for any correlational study, it is possible that there is an unknown factor that causes smaller maturation size and is positively correlated with prevalence.

Reproducing early as an adaptation against parasitism could be a result of natural selection against snails that delay maturation in populations that are at a high risk of parasitic castration. How likely is the potential for local adaptation in these snails? Other better studied snail species have a heritable component to maturation size suggesting that there may be genetic material on which natural selection can act (Richards and Merrit 1975). There is also reasonable potential for genetic isolation among snail populations. Horn snails occupy coastal salt marshes and bays separated by expanses of exposed coastline. Eggs hatch into non-planktonic (crawl-away) larvae and adults are sedentary (Race 1981). Therefore, gene flow is probably low between marshes and among sites within a marsh. This direct development increases the likelihood for local adaptation (Endler 1986, Yamada 1989). For the two populations involved, the reciprocal transplant experiment conclusively shows that there was an effect of natal habitat on maturation size. The lack of replication among populations leaves open the possibility that this could be a random genetic difference between the two populations and it is not possible to conclude that this difference exists for all the populations surveyed. However, in conjunction with the pattern observed among several marshes, this result is consistent with the hypothesis that maturation size may be heritable and under selection from parasitic castration. Nevertheless, the limited duration of this transplant cannot determine that the observed variation in maturation size is genetic. Such apparent genetic differences could be environmentally determined through maternal effects or an early commitment to a life-history strategy. As an example, in a common environment, snails (*Lymnaea elodes*) from a temporary pond mature earlier and smaller than snails from a permanent pond, but these differences disappear after one generation (Brown 1985).

Alternatively, it is possible that phenotypic plasticity determines the association between maturation size and prevalence such that early juvenile or egg stages make a developmental switch based on an assessment of their perceived risk of castration. There are a number of reasons to suspect phenotypic plasticity in this case. Phenotypic plasticity should evolve when the environment is highly variable (Bradshaw 1965), and some year to year variation in infection rates occurs in some *Cerithidea californica* populations (W. Sousa, pers. comm.). Furthermore, it is possible that snails might be able to assess the immediate risk of parasitism. Snails could use cues such as penetration from trematode miracidia or be able to detect the presence of trematode cercariae. Additionally, since parasitized snails do not show copulatory behavior (Sousa 1983), interactions among snails might enable unparasitized snails to determine the prevalence of infection. For phenotypic plasticity to explain the observed pattern, it is necessary that snails commit to a certain life-history strategy when they are still quite small. This possibility is not as improbable as it might seem. Smith-Gill (1983) demonstrated that environmental cues can trigger a series of irreversible developmental switches in very young individuals. For example, when exposed to echinostome miracidia, young snails (*Biomphalaria* spp.) grow slower than unexposed snails whether or not the exposed snails become infected (Mueleman 1972, Kuris 1980). This suggests that environmental variation can induce life-history strategies earlier in ontogeny than one might expect. Unfortunately, from this evidence, it is impossible to conclude whether variation in the size of maturity is plastic or if it is a genetic response to variation in selective pressures among populations. There is reason to expect either or both. To fully distinguish between the roles of phenotypic plasticity and genetic variation may require studies of short lived freshwater snail hosts appropriate for rearing in the laboratory or long term field experiments where rates of parasitism are manipulated among replicated habitats.

As an adaptation against parasitic castration, early maturation appears to be a reasonable alternative to avoidance or resistance. These other adaptations against parasitism may be ineffective or costly. For instance, behavior to avoid parasitism can carry the cost of reductions in food (Moore 1983, Lafferty 1992), whereas host resistance may interfere with competing physiological needs (Palmer 1983), and reduce competitive ability (Minchella and LoVerde 1981, 1983). Hosts that reproduce earlier do not live longer lives, nor are they better at acquiring mates or obtaining resources. In this sense, early maturation is unique from other adaptations against parasitism in that it does not serve to

help the host defeat or elude parasites; it allows the host to cope with them.

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