Predator-Induced Life-History Shifts in a Freshwater Snail

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The snail *Physella virgata virgata*, a widely distributed freshwater pulmonate, was observed to change its life-history characteristics in the presence of the crayfish *Orconectes virilis* in spring-fed Oklahoma streams. These changes were apparently initiated by a water-borne cue released when crayfish fed on conspecific snails. In the presence of the cue, snails exhibited rapid growth rates and little reproduction until they reached a size of about 10 mm after 8 months. In the absence of the cue, snails typically grew to about 4 mm (3.5 months) and then began reproduction. The chemically inducible shift indicates that the life histories of these snails are phenotypically plastic. By increasing the variance associated with size and age of maturity, prey may increase the likelihood of coexisting with seasonal predators.

TRADEOFFS IN LIFE-HISTORY CHARACTERISTICS often determine survival and fitness of individuals (*1*). For example, the pattern of energy allocated to growth versus reproduction, size versus number of offspring, and growth versus the timing of metamorphosis will determine the short-term gain from immediate reproduction and the probability of survival to achieve future reproduction (*2*). Understanding allocation patterns is of importance to the synthesis of life-history evolution. Most studies of animals addressing this issue have concluded that genetic differentiation accounts for most of the observed differences among populations (*3*). Phenotypic plasticity (*4*) represents an alternative to the traditional genotypic selection explanation, with genotype and environment interactions giving rise to either discretely or continuously varying phenotypes (*5*). Plasticity of life-history patterns has been reported, primarily for plants (*6*) and invertebrates (*7*), though some data also exist for a few vertebrate groups (*8, 9*). The environmental factors thought to "cue" the life history responses include nutrients (*5*), food (*10*), photoperiod (*11*), disturbance (*9, 12*), and conspecific crowding or social structure (*13, 14*).

Although predators are known to have significant effects on prey behavior (*15*), prey population sizes (*16*), and prey morphologies (*17*), only a few studies suggest that predators significantly affect life-history characteristics directly (*3, 14, 18, 19*). Of these, only algae, higher plants, and a colonial bryozoan have been shown to exhibit phenotypically plastic responses in life-history characters to grazers (*14, 19, 20*). In all of these cases, grazing on asexual individuals results in the induction of sexual reproduction. We report a novel response to a predator, in which life-history characteristics (age and size at first reproduction and longevity) of a nonclonal, freshwater snail species show a phenotypically plastic response to a water-borne chemical factor excreted by crayfish when they forage on snails.

The snail *Physella virgata virgata* is a widely distributed freshwater, pulmonate snail. Members of the subclass Pulmonata are secondarily adapted to freshwater and show adaptations to variable environments (*21*). They exhibit short life cycles, mature at a young age, and have a short reproductive period (*3, 10, 22*). A variety of predators (for example, fish, insects, birds, and crayfish) include snails in their diets. Crowl (*23*) reported two different life-history patterns for these snails inhabiting spring-fed streams. These differences were correlated with the presence or absence of crayfish. Snail populations in streams without crayfish exhibited the typical life-history pattern of rapid growth up to about 4 mm (shell length), at which time growth rate decreased and reproduction began. Snail longevity ranged from 3 to 5 months in these populations. When crayfish were present, an increase in the age and size at maturity was observed, with egg production beginning at a size of 7 to 10 mm. Longevity ranged from 11 to 14 months for these individuals.

Two hypotheses might explain these observations. First, the differences in life histories might be a result of genetic differentiation between populations, due to long-term exposure to crayfish predation. Because crayfish feed selectively on the smallest

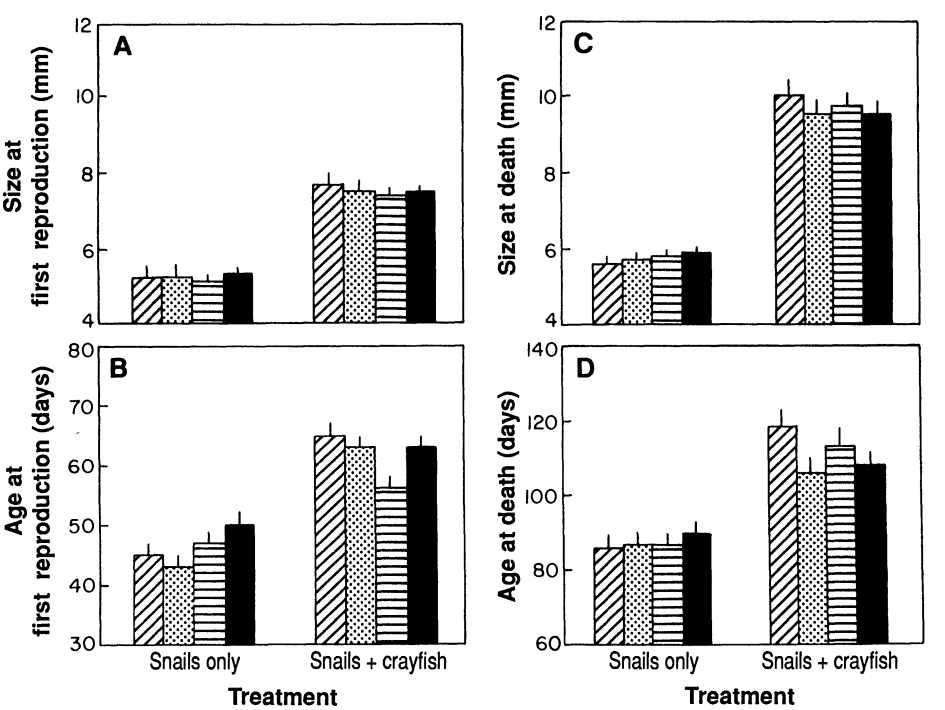

Fig. 1. Size and age at first reproduction (**A** and **B**) and death (**C** and **D**) for all four snail populations for the first experiment with snails only and crayfish + snails as the two treatments. Bars are means based on 12 replications with three specimens for each snail population and lines are 1 SE. A two-way analysis of variance resulted in only the predation treatment having a significant effect on any of the dependent variables [$F(1,4) = 608.3$, 229.4, 1557.6, and 162.6; $P = 0.0001$, 0.0001, 0.0001, and 0.0002 for each dependent variable in (A) to (D), respectively]. The source of the snail population (whether crayfish were present in the stream or not) and the interaction between snail source and predator treatments were not significant. All tests were run at the $P = 0.012$ level, because four separate analyses were conducted for each experiment (*25*).

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snails (*23*), juvenile mortality is high in the presence of crayfish, and current life-history theory predicts that maturity will be delayed (*24*). Alternatively, the observed differences might represent a phenotypically plastic response to the presence or absence of crayfish. A number of invertebrates are known to exhibit morphological changes or avoidance behaviors in the presence of predators or predator chemicals (*15, 17, 20, 25*).

To test the hypothesis of plasticity versus genetic differentiation of local populations, we conducted flow-through laboratory experiments using snails from two streams with crayfish (C1 and C2) and two streams without crayfish (NC1 and NC2) in a cross-classified design with a variety of water-source treatments (*26*). The first experiment included two water-source treatments: (i) crayfish and snails present and (ii) snails only. We recorded age and size at first reproduction, average age and size at mortality, and before and after reproduction growth rates and analyzed these data using two-way analysis of variance (*27*).

In the first experiment, snails in containers that received water with crayfish and snails together (predation) were significantly larger and older at first reproduction and at death than snails that received water containing only snails, independent of the source of the snail population (Fig. 1). Although there was considerable variation between populations, the majority of variance associated with these life-history parameters was primarily due to the presence or absence of crayfish in the water source.

To gain more specific information on the nature of the chemical factor that elicited the observed life-history switches, a second experiment was conducted that included four water-source treatments: (i) snails only, (ii) crayfish only, (iii) snails and crayfish separated (no predation), and (iv) crayfish and snails together (active predation). Only the treatment with crayfish and snails together, in which snails were actively preyed on, resulted in delayed age and size of maturation and increased longevity. As in the first experiment, the source of the snail population did not affect the outcome (Fig. 2), which contradicts the hypothesis that differences were due to different genotypes between the populations.

Our results suggest that snails are capable of detecting a chemical cue that results from crayfish actively foraging on snails (*28*). In the presence of this cue, snail life-history patterns are altered with both the age and size of maturation being delayed. This pattern is consistent with the predictions of a variety of age-specific life-history models when juvenile mortality is greater than adult mortality (*24*). Crayfish predation rates decrease as snail size increases, with a size threshold occurring at about 10 mm for these snails (*23*). Thus, by delaying the onset of reproduction and growing to a larger size, snails decrease mortality due to size-specific predation.

A number of studies suggest that waterborne chemicals may be important in determining activity patterns, morphologies, and life-history patterns in a variety of prey taxa (*20, 25, 29*). Phenotypic plasticity, as an antipredation strategy, while well documented for plants, has now been shown in a colonial and solitary animal. The rapid responses by snail prey that we observed suggest that the application of simple predator-prey models to biologically control snail populations may be of limited use. Our results also point out the need for caution in interpreting changes in gastropod shell sizes in systematics and paleoecological studies. Finally, we suggest that selection for phenotypic plasticity may be a more effective adaptation for avoiding predation than genetic differentiation of local populations. This will be particularly true if predation pressure varies seasonally, but in a manner that is not easily detected by relying on environmental cues (for example, temperature regimes and light cycles).

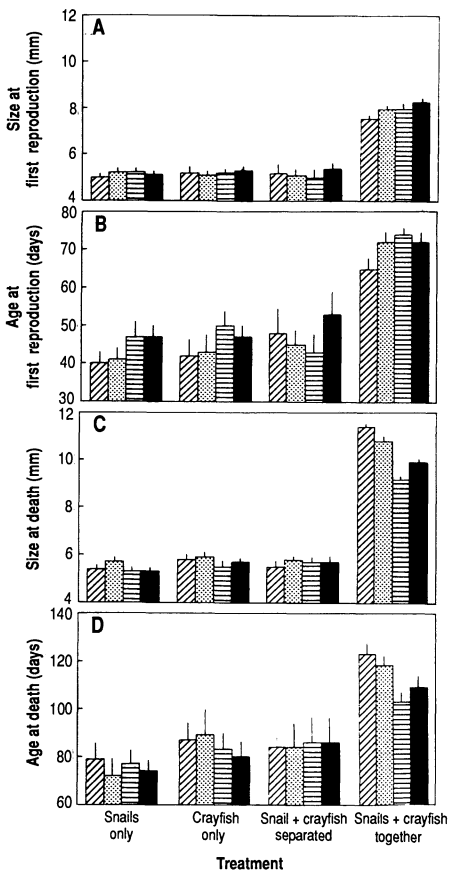

Fig. 2. Size and age at first reproduction (**A** and **B**) and death (**C** and **D**) for all four snail populations for the second experiment with the following treatments: snails only; crayfish only; crayfish + snails, separated to eliminate predation; and crayfish + snails, with active predation. Bars are means based on six replications with three specimens for each snail population and lines are 1 SE. A significant predator treatment effect was detected for all dependent variables [$F(3.8)$ = 308.0, 58.9, 451.6, and 136.4; P = 0.0001, 0.0001, 0.0001, and 0.0002 for each dependent variable in (A) to (D), respectively]. The REGWQ multiple-range tests resulted in significant differences between the snail + crayfish with active predation treatment and the rest of the predator treatments for all dependent variables. A significant snail source effect was detected only for the age at death [$F(1,8)$ = 11.3, P = 0.0098]. No significant interactions between snail source and predator treatments were detected.

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26. The experimental setup for both experiments consisted of 80-liter reservoirs that contained water from a stream without crayfish and the appropriate predator treatment (see below). Water from these reservoirs was gravity-fed through 1-mm diameter plastic tubing into 0.2-liter glass dishes that contained three snails from one of the source populations. Water was circulated through the dishes approximately three times per day. All snails were 2 mm in size and approximately 10 days old at the initiation of each experiment. Snail sizes and reproductive output were monitored every 7 to 10 days. For the first experiment, predator treatments consisted of snails only and snails plus one crayfish together. Each treatment combination was replicated 12 times. In the second experiment, predator treatments included snails only, crayfish only, snails plus crayfish in the same reservoir but separated by a 2-mm mesh net (to eliminate predation), and snails plus crayfish together (not separated so predation did occur). Each treatment combination was replicated six times. In both experiments, ad libitum amounts of boiled spinach were added to all reservoirs and snail dishes every 3 to 5 days as an additional food source for both crayfish and snails. All experiments were conducted in environmental chambers with a 12/12 light/dark cycle and 18°C temperature.
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Double Fertilization in *Ephedra*, a Nonflowering Seed Plant: Its Bearing on the Origin of Angiosperms

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Double fertilization and the associated formation of endosperm have long been considered unique and defining characters (autapomorphies) of the angiosperms. During normal fertilization in *Ephedra nevadensis*, a nonflowering seed plant, fusion of a second sperm nucleus with the ventral canal nucleus occurs regularly within the egg cytoplasm. The occurrence of double fertilization in *Ephedra* assumes added significance in light of its critical phylogenetic position as a basal member of the most closely related extant group of seed plants (Gnetales) to angiosperms. Thus, double fertilization in angiosperms and *Ephedra* may represent an evolutionary homology.

THE PROCESS OF DOUBLE FERTILIZATION in angiosperms, whereby one sperm fertilizes an egg while a second sperm fuses with the polar nuclei of the female gametophyte (embryo sac), was first reported by Navashin in 1898 (*1*). Subsequently, double fertilization and the associated formation of polyploid endosperm have been considered unique and defining characters (autapomorphies) of the angiosperms (*2–6*). Indeed, many plant biologists have suggested that double fertilization and endosperm represent significant reproductive features that are intimately associated with the ecological and evolutionary success of flowering plants (*7, 8*). Although considerable attention has been paid to the biological or "adaptive" significance of double fertilization and endosperm (*9*), relatively little work has been directed toward understanding the evolutionary origins of these important and apparently unique features of sexual reproduction in flowering plants.

Since the initial discovery of double fertilization in angiosperms, there have been occasional, poorly substantiated reports of anomalous double fertilization–like events in nonflowering seed plants, particularly the genus *Ephedra* (*10–15*). The possible occurrence of double fertilization in *Ephedra* is significant in view of recent phylogenetic studies of seed plants (*6, 16*). These cladistic analyses indicate that the Gnetales (*Ephedra, Gnetum*, and *Welwitschia*) are monophyletic, form part of a larger clade that includes angiosperms, and are more closely related to flowering plants than is any other extant group of seed plants. Finally, *Ephedra* is basal within the Gnetales and has retained many primitive characteristics of the group. Thus, *Ephedra* occupies a critical position in the phylogeny of seed plants. Character traits (such as double fertilization) that are shared by angiosperms and Gnetales are potentially evolutionarily homologous (synapomorphous), having been inherited from a common ancestor.

Extensive collections of *Ephedra nevadensis* took place in 1987 and 1988 from populations growing north of Tucson, Arizona. Ovules were dissected, fixed in glutaraldehyde, dehydrated, and embedded in glycol methacrylate. Each ovule was serially sectioned at 3 to 5 μm into several hundred sections. Complete sets of serial sections ensured that all nuclei from a specific male gametophyte and archegonium could be accounted for and correctly interpreted.

Within hours of pollination, the central cell nucleus, located at the micropylar end of the central cell, divides to produce a ventral canal nucleus and egg nucleus. There is no evidence of wall formation between the two daughter nuclei. The ventral canal nucleus remains in situ at the extreme micropylar and vacuolate end of the egg cytoplasm. The incipient egg nucleus migrates in a chalazal direction where it enters and becomes immersed in an unusual columnar zone of cytoplasm, which has been shown to be rich in mitochondria and plastids in *E. distachya* (*17*).

In *E. nevadensis*, the ventral canal nucleus

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