

Comparative long-term mark-recapture studies of guppies (*Poecilia reticulata*): differences among high and low predation localities in growth and survival

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Life history theory predicts that high extrinsic mortality rates will cause the evolution of earlier maturity and increased reproductive effort. Guppies that co-occur with predators support these predictions because they attain maturity at an earlier age and have higher levels of reproductive effort than their counterparts from localities that lack predators. In the past, we used short term (12 day) mark-recapture studies to show that guppy populations that co-occur with predators do in fact have higher mortality rates than those that do not. Here we extend this result to long term mark-recapture studies with a single recapture interval of over 200 days. We show that the recapture probabilities after these longer intervals are very similar to what one would predict based on the short term studies. Because of the multiplicative nature of mortality rate, the differences in recapture rates in guppies from low as opposed to high predation sites are now much more dramatic, on the order of 20 to 30 fold after 200+ days, as opposed to being around 15% higher after 12 days. The earlier short-term studies also revealed that guppies from high predation localities grow faster, in part as an indirect effect of predators because they reduce guppy population densities and increase per capita food availability. The long-term studies reported here yield the same result, but the difference between high and low predation localities is again far more dramatic as a consequence of the longer duration of the recapture interval. These observations, in combination with those of the earlier work, support the hypothesis that the increased mortality that accompanies predation represents a plausible mechanism that causes the evolution of the observed differences in life histories; however, the confounding of mortality rate and growth rate also suggests that more complex life history models that include density regulation and eco-evolutionary interactions may provide a better explanation for life history evolution in guppies.

Introduction

The definition of cause and effect in the study of evolution by natural selection demands the characterization of the mechanisms of selection. In our work on natural populations of guppies from the island of Trinidad, we are interested in evaluating the mechanism of selection in comparisons among populations. We have *a priori* reason to think that there are differences among populations in mortality rate that are caused by differences in risk of predation and that this extrinsic source of mortality causes the evolution of life history and other traits (Endler 1995). These populations vary in their risk of predation as a function of the species of predators that they co-occur with. The argument for predator-induced mortality was traditionally based on the widespread correlation between guppy morphology, life histories and behavior. For life history evolution, there are specific links between how the life history is expected to evolve and the magnitude and age-specificity of predator-induced mortality (Charlesworth 1994, Abrams & Rowe 1996), so we have evaluated this presumed mechanism by estimating the comparative, size(age)-specific mortality rates of guppies from high and low predation environments (Reznick *et al.* 1996a). Our earlier conclusions were based on mark-recapture studies estimated over a short time frame (12 days). Here we report on studies carried out over time intervals of up to 240 days and show that the long-term trends are well-predicted by the shorter-term studies. We also show that the high mortality rates of guppies from high predation environments are correlated with higher growth rates, which plays an important role in alternative hypotheses for how and why life histories have evolved in these fish.

In high predation environments, guppies co-occur with predators like the pike cichlid *Crenicichla alta* that frequently prey on guppies and often target adult size classes. In low predation environments, guppies co-occur only with the killifish *Rivulus hartii*, which occasionally preys on guppies and preys almost exclusively on small, immature size classes. This contrast between high and low predation environments

is repeated in many drainages. Low predation environments are often separated from high predation environments by barrier waterfalls, so the two can be found in close proximity to one another in streams that are very similar in structure. We have previously shown that field caught guppies from high predation environments are smaller at maturity, produce more and smaller offspring per litter, and have larger litters relative to their body sizes than guppies from low predation environments (Reznick & Endler 1982, Reznick 1989, Reznick *et al.* 1996b). In complementary laboratory studies, we showed that guppies from high predation environments are younger at maturity and that the remaining differences in life histories persist even after two generations in a common environment (Reznick 1982, Reznick & Bryga 1996). We have also shown that it is possible to transplant guppies from a high predation site over a waterfall into a previously guppy-free low predation site and that these same life history patterns will evolve in as little as 11 years (Reznick & Bryga 1987, Reznick *et al.* 1990). The combination of these comparative studies and experiments has provided strong support for theories that predict how life histories will evolve in response to differences in age-specific extrinsic mortality rate (Reznick *et al.* 1990).

Our mark-recapture studies exploit the pool-riffle structure of some streams because guppies tend to congregate in pools and have restricted movement among pools. We are able to catch virtually all guppies within a pool. Here we employ similar methods, but with the goal of evaluating the longer-term consequences of the differences between high and low predation environments, particularly mortality rate and growth rate. We report on mark-recapture studies of four natural populations of guppies, based on a single, long-term mark-recapture interval. The special challenge of these fish include individually marking small individuals (as small as 10 mm standard length), then recapturing and measuring them in natural streams that are often subject to flooding during the rainy season; a consequence of flooding is the potential movement of individuals over long distances and the loss of marked individuals.

Methods

We collected the entire population of guppies from a single large pool in two high predation and two low predation streams using hand nets. In each case we chose a pool that held a large population of guppies and that was well defined by a physical barrier, either a small waterfall or steep riffle, on the up- and downstream side. We chose such pools because we had found previously that such barriers restrict the immigration and emigration of guppies. We argue that we can catch virtually all guppies in these settings based on previous mark-recapture studies in which we recorded the numbers of marked fish that we were able to catch on the successive days of recollecting at the same site. For example, at one site (Reznick *et al.* 1996a: table 2B) we recaptured 90 marked fish on the first day of recollecting, one on the second day and none on the third day. In two other sites (Reznick *et al.* 1996a: table 2A) we caught 108 and 216 marked fish on the first day and no marked fish on a second visit either one or two days later. We also performed two studies that included multiple release-recapture intervals that allowed a formal estimation of the probability that a fish was alive but not recaptured during a single visit using the program MARK (White & Burnham 1999). These studies were more than an order of magnitude larger than the former studies in terms of both the number of pools sampled and the number of marked fish in the study, which resulted in a dilution of the intensity of effort in recollecting each pool. Even when working on this larger scale, our estimated average probabilities of recapturing an individual on a single visit if it was alive were 96.7% and 91.7% for the two sites (Bryant & Reznick 2004). The present studies were executed in the same fashion and with the same intensity of effort as by Reznick *et al.* (1996a). It is on the basis of this earlier research that we argue that we are able to capture virtually all fish within a restricted area.

Our two high predation sites were the Ceniza and Aripo Rivers. Our two low predation sites were tributaries to the Aripo and El Cedro Rivers. Both low predation sites are ones that had previously contained only the killifish *Rivulus hartii* and no guppies. Guppies were intro-

duced to the Aripo Tributary in 1976 by John Endler and to the El Cedro Tributary in 1981 by David Reznick. These sites have since been used to evaluate the evolution of guppy life histories and male coloration in response to changes in extrinsic mortality rate (Endler 1980, Reznick & Bryga 1987, Reznick *et al.* 1990, Reznick *et al.* 1997). In the Aripo River, we performed the same mark-recapture process in two successive time intervals, so we have data from a total of three mark-recapture intervals for high predation localities and two for low predation localities.

Our marking protocol for three of the four studies (El Cedro, Aripo Tributary, Aripo River) was the same as employed in our initial, short-term mark-recapture studies (Reznick *et al.* 1996a). We used a commercially available elastomer (Northwest Marine Technologies) and marked the fish with a subcutaneous injection in the caudal peduncle. Each fish received a single mark. We used two colors and eight different locations (above or below the vertebral column, anterior or posterior, left or right), which enabled us to uniquely mark sixteen different size classes of fish. We uniquely marked each mm size class up to 24 mm. No larger fish were encountered in our initial collections. The smallest size class was 10 mm for the studies on the Aripo Tributary and El Cedro Rivers and for the second of the Aripo River studies. The smallest size class for the first study of the Aripo River was 12 mm. All fish in the Ceniza study received two marks (eight possible positions, four possible colors) that uniquely identified each individual. We also gave all mature males the same mark in a color that distinguished them from females and immature males. All fish were anaesthetized with tricaine methane sulfonate when being injected, then were held in medicated water for at least 24 hours after injection to prevent fungal or bacterial infections that might result from handling or injection. They were then reintroduced to the site of capture. All lengths were measured from the tip of the lower jaw to the outer margin of the hypural plate.

We recaptured guppies from the release sites after intervals of 205 to 237 days (Table 1). When recollecting, we also sampled at least the next two discrete pools up- and downstream from the release sites to search for émigrés. Note that,

because there was only one recapture interval, we cannot independently estimate the probability of survival versus the probability of being caught if the individual was alive and remained within the sampling region. Individuals that emigrated beyond the area sampled would be included with the “not recaptured and presumed dead” subset of our population. Because our recapture effort was comparable to the effort made when initially collecting the population, we assume that the probability of recollecting any marked individual that was present was exceedingly high. These new collections were dominated by unmarked fish, presumably those who had migrated into the study site or had been recruited during the interval between release and recapture. We did not enumerate the unmarked individuals.

Statistics

Our data analyses included an evaluation of growth rate, estimated as the difference in the size of individuals when recaptured and the mean in each mm size class when originally marked. The relationship between initial size and growth increment typically has a negative slope, meaning that the rate of growth is slower in larger size classes. This relationship is curvilinear (concave upward) because individuals with larger initial sizes had progressively smaller proportional increases in size. We found that a quadratic regression [initial size + (initial size)²] provided an excellent fit to the growth increment (y-axis) by initial size (x-axis) relationship (Fig. 1); the residuals

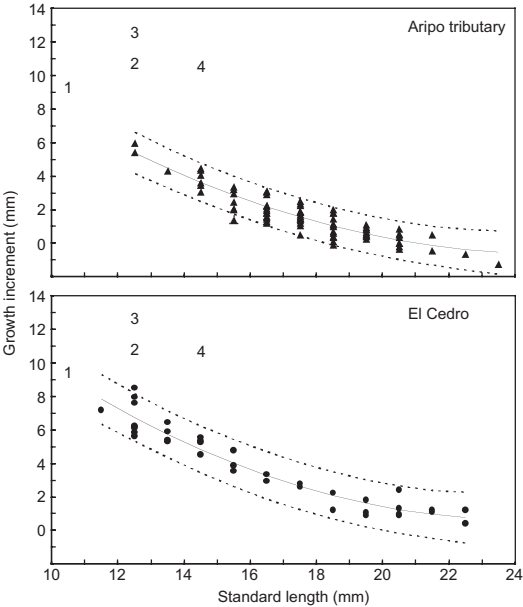


Fig. 1. The growth increments, as a function of initial size, of the fish from the two low predation localities. The fitted curves are based on a quadratic equation with the initial size as the independent variable and the growth increment as the dependent variable. We have superimposed the growth increments of the four recaptured individuals from the two high predation localities for purposes of comparison. The number of standard error units between these observed values and the values predicted on the basis of the growth increments in the low predation localities are reported in the text.

from this curve fit were normally distributed and homoscedastic. This relationship between initial size and growth increment in turn provides a perspective for evaluating the growth rates of fish in high versus low predation localities. We used

Table 1. Details for the five mark-recapture studies. Two consecutive mark-recapture studies were done on the Aripo River (high predation) and one each was done on the Ceniza River (high predation), Aripo Tributary (low predation) and El Cedro River (low predation). We record below the date on which marked fish were released, the date of recapture, the number of elapsed days, the number of marked mature males that were released and recaptured and the number of marked adult females and immature fish that were released and recaptured.

Site	Date released	Date recaptured	Duration (days)	Males – #marked/#recaptured	Females + immatures – #marked/#recaptured
Aripo A (high predation)	12 Sep. 1997	6 May 1998	235	20/0	82/1
Aripo B (high predation)	8 May. 1998	29 Nov. 1998	205	36/0	118/1
Ceniza (high predation)	11 Sep. 1997	30 Apr. 1998	229	29/0	108/2
Aripo Tributary (low predation)	12 Sep. 1997	1 May 1998	230	52/3	220/81
El Cedro (low predation)	30 Apr. 1998	25 Nov. 1998	209	51/0	225/39

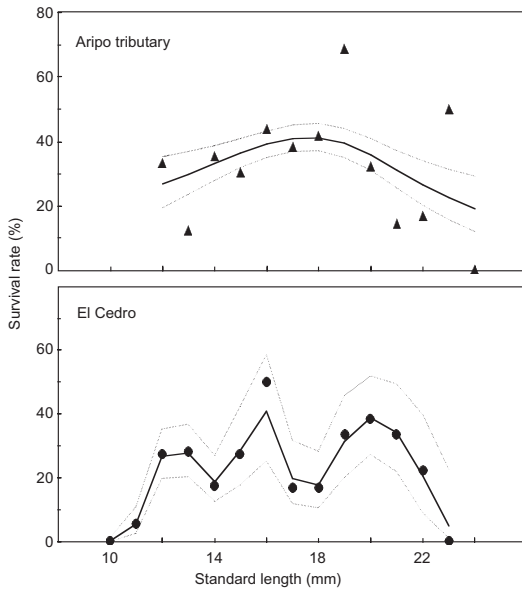


Fig. 2. Cubic splines fitted to the plot of the probability of recapture (y-axis) and the initial size class for the two low predation localities.

the analysis of covariance, with initial size and (initial size)² as a covariates, to make comparisons among populations in the size of the growth increment. We also evaluated the overall probability of recapture, then the probability of recapture as a function of initial size. The exact dates for release of marked fish, the first recapture date, the number marked and released and the number recaptured are summarized in Table 1. Size-specific recapture probabilities were characterized with cubic splines (Schluter 1988).

Results

Recapture probability

We did not find any émigrés at any of the study sites. A likely explanation is that the frequency of emigration from pools with natural up- and downstream barriers is relatively low. When combined with the relatively low probability of survival over a seven to eight month time interval, it is possible that no émigrés survived long enough to be recaptured. A second possible explanation is that marked fish emigrated beyond the portion of stream that we searched for émigrés.

The overall probability of recapture of marked female and immature fish in our two low-predation sites was 17.3% (39/225) for the El Cedro River and 36.8% (81/220) for the Aripo Tributary. We did not recatch any of the 51 marked mature males in the El Cedro River and only 3 out of 52 marked males on the Aripo Tributary. We only recaptured four out of a total of 393 marked fish (approximately 1%) in our two high predation sites (Table 1).

Only the low predation sites yielded sufficient sample sizes for further survival analysis. In both cases, we find that the shape of the cubic spline is concave downwards, or that the probability of recapture increased from 12 mm to approximately 16–18 mm and decreased thereafter (Fig. 2).

Growth rate

In low predation sites, individuals that were initially in the 12–12.99 mm size class grew to an average of 18.22 mm ($n = 2$) in the Aripo Tributary and 19.26 mm ($n = 8$) in the El Cedro River. The growth increments tended to be 1 to 2 mm larger across all size classes in the El Cedro River. Since the recapture interval was shorter in the El Cedro River (Table 1), such a direct comparison will underestimate the differences in growth rate. There were not significant interactions between initial size ($F_{1,112} = 0.27, p = 0.60$) or (initial size)² ($F_{1,112} = 0.23, p = 0.63$) and growth increment. An analysis of covariance that excluded these interactions revealed that each of the covariates was significant [initial size: $F_{1,114} = 70.0, p < 0.0001$; (initial size)²: $F_{1,114} = 35.0, p < 0.0001$]. It also revealed that the mean growth increment was significantly larger in the El Cedro than in the Aripo Tributary ($F_{1,114} = 73.6, p < 0.0001$; least square mean increments: El Cedro = 3.12 mm, Aripo Tributary = 1.98 mm).

All of our recaptures in high predation localities were associated with much larger growth increments (Fig. 1) than seen in the low predation localities. In the Ceniza River, both recaptured females were greater than 25 mm long, which is larger than the largest individuals seen in our low predation sites during the course of this

study, even though their initial lengths were only 12 and 14 mm. In the Aripo River, one individual grew from 12 mm to 23.15 mm. A second individual grew from 10+ mm to >19 mm. The growth increments for the first three fish were much larger than observed for comparable initial sizes in the low predation sites (Fig. 1). The fourth fish's initial size of 10 mm was smaller than the initial sizes of any of the recaptured fish from the low predation localities so it could not be directly compared with them. We evaluated whether or not the three recaptures of fish with initial sizes of 12 and 14 mm implied significantly higher growth rates in high predation localities by comparing them with the standard error for growth increment in equal sized fish from the two low predation localities. We performed two such analyses. In the first, we ignored the differences in recapture interval, which implicitly assumes that all fish had attained an asymptotic body size within the shorter interval. In the second analysis, we transformed the data into an average growth increment per day, which assumes that all fish sustained growth along a quadratic trajectory throughout the time interval. The main source of concern in the two analyses is the shorter recapture interval for the El Cedro River (209 days) than for three of the four individuals from high predation localities (229 and 235 days). The first analysis would tend to exaggerate the growth rate differences while the second would tend to reduce them, so the two together represent boundary conditions. We found that the results were qualitatively the same either way. In the first type of analysis, the growth increment of the three high predation recaptures ranged from 8.2 to 11.3 standard errors greater than the predicted growth increment for equal sized fish from the Aripo Tributary and 6.5 to 9.5 standard errors above the predicted values for the El Cedro River. Our analyses of growth rate on a per day basis yields similarly higher values from the high predation recaptures: 9.4 to 10.6 SE above predicted rates for the Aripo Tributary and 7.3 to 8.3 SE above predicted daily growth for El Cedro River. These three observations suggest that guppies from these high predation localities grow significantly faster than those from low predation localities, although the limitations of

such long-term studies admit other alternatives, as discussed below.

Discussion

The probabilities of recapture in these long-term studies are close to what one would predict if we extrapolated our average short-term probabilities of recapture at high and low predation localities to the time interval of the current studies; they reaffirm our earlier result, which is that guppy populations in high predation sites experience higher mortality rates. They also graphically illustrate the substantial long-term consequences of what may seem like subtle differences in mortality rate in the near-term. With a mark-recapture interval of 12 days (Reznick *et al.* 1996a), the average probability of recapture of immature and female fish that were 12 or more millimeters long when marked was 78% for high predation localities and 90% for low predation localities. If we project these same mortality rates to the time intervals of the current study, then they predict a 10- to 20-fold difference in survival between high and low predation sites. For high predation sites, they predict a recapture rate of 0.8% to 1.5%, which brackets our average recapture probability for the three high predation assays (four out of 393 marked fish). The predicted recapture probabilities for the two low predation sites is 16% for the El Cedro and 13% for the Aripo Tributary, which is actually lower than the observed recapture probabilities. In the case of the Aripo Tributary, a 95% probability of survival over a 12 day interval projects to the observed recapture probability of 37% while for the El Cedro River a 90.4% probability of survival for a 12 day interval projects to the observed probability of recapture of 17.3%. The projected 12 day survival rate of 95% for the Aripo Tributary falls at the upper end of the range that we observed for individual mark-recapture studies in our earlier work (Reznick *et al.* 1996a). The observed recapture probability after 12 days for males from high predation sites was only 57%, which projects to essentially no probability of recapture after the longer time intervals of the current study, which is what we observed. The observed recapture probability after 12 days of

males from low predation sites was 77%, which projects to an approximately 1% probability of recapture in the current study. We did not recatch any mature males on the El Cedro River, but recaptured three out of 52 marked mature males on the Aripo Tributary. This latter figure is consistent with the higher probability of recapture of immatures and females at this locality. We make no claim for these long-term studies providing precise estimates of the probability of survival because they cannot account for either emigration or the probability of being alive and resident but not recaptured. Nevertheless, the raw recapture probabilities and their consistency with values that one would predict on the basis of short-term studies suggests that there was little permanent emigration from these sites over the time interval of these studies.

The long-term nature of the study also admits the possibility that some individuals died due to intrinsic causes. Our laboratory studies of senescence in guppies (Reznick *et al.* 2004) show that they have median lifespans that range from 699 to 1031 days, depending on population and treatment group. Bryant and Reznick (2004) showed that size is well correlated with age. The shape of the recapture probability in the low predation sites (Fig. 2) thus implies that the mortality rate of the oldest marked fish was higher than for younger fish, which is in turn consistent with senescence. Our short term mark-recapture studies on a larger number of localities yielded similar results (Reznick *et al.* 1996a). On the basis of these two results, we hypothesized that guppies from low predation environments are sufficiently long-lived for them to experience an age-specific acceleration in intrinsic mortality rate with age, which is one definition of senescence. In a different study, we formally tested this hypothesis on the El Cedro River by showing that there is a significant acceleration in mortality rate in older age classes. This study was a long-term, multiple recapture study on individually marked fish from the same site on the El Cedro River as the current study (Bryant & Reznick 2004). Taken together, these observations suggest that guppies from low predation environments in nature frequently live long enough to experience senescence in the form of an age-specific acceleration in mortality rate.

The current growth increment results graphically illustrate what are likely to be the long-term consequences of the differences in growth rate seen in the earlier short-term mark-recapture study (Reznick *et al.* 2001). The earlier paper reported that guppies from high predation localities have higher growth rates and larger asymptotic body sizes than those from low predation localities. Guppies from high predation sites are also found at lower population densities and the populations are dominated by smaller individuals, which is what is expected given their higher birth and death rates (Reznick *et al.* 1996). Finally, the earlier study showed that resource availability was higher in high predation environments. The observed differences in growth rate in the current and past studies are thus consistent with guppies having higher levels of food availability in high predation localities which are in turn interpreted as being in part an indirect effect of predators (Reznick *et al.* 2001) because predators reduce the population density of guppies. This means that the way guppy life histories evolve may be shaped by a confounding of differences in mortality rates and differences in density and resource availability (Reznick *et al.* 2001).

An alternative interpretation to our results is that these differences in growth are caused by genetic differences in growth rate between high and low predation guppies rather than differences in resource availability. Arendt and Reznick (2005) found in the context of a common-garden laboratory study on the grand-children of wild caught guppies that guppies from high predation localities tended to have higher growth rates than those from low predation localities. Seeing such differences in such a controlled environment suggests that there is a genetic basis to the higher growth rate of high predation guppies; however, the magnitude of the growth rate difference measured in the lab ranged from one half to one fifteenth of the average difference in growth rate between high and low predation guppies in the field. We thus consider the differences in primary productivity and food availability observed by Reznick *et al.* (2001) to be the more important explanation for the higher growth rates of guppies from high predation environments. It is also possible that there are differences in the sus-

ceptibility of fast versus slow growing guppies to predation; any bias created by such selective predation would only be an issue if slow-growing guppies are more susceptible to predation in high predation localities and/or fast growing guppies are more susceptible to predation on low predation localities. If such a bias existed, it would cause far less distortion in the results in a short-term mark-recapture study than is possible in a longer-term study, such as this one, because the proportion of fish that die in short term studies is much smaller. Since we obtained consistent growth rate results in both long- and short-term mark-recapture studies and since we also found lower population densities of guppies and higher productivity in high predation localities, we strongly favor the interpretation that the observed differences in growth increments are the product of higher growth rates that are caused by higher per capita food availability.

In summary, the results of the current study support those of our earlier work, in which we documented that guppies that live with predators suffer higher mortality rates but also have higher growth rates (Reznick *et al.* 1996a, 2001). The new element here is that the differences between high and low predation localities were measured over a much longer time interval and have shown that the short-time estimates are reasonable predictors of long-term differences in mortality and growth. Because of the multiplicative nature of differences in mortality rate, the new results also show how dramatic the effect of living with predators can be since the 15% reduction in survivorship over 12 days results in a 20 to 30 fold difference in survivorship after seven to eight months. The confounding of high mortality rates with high growth rates invokes the dilemma of the past concerning the role of predators in shaping life history evolution in guppies, which is the extent to which their impact is their direct influence on mortality rate versus an indirect effect that is mediated through resource availability and density regulation. Theory has shown that the confounding effects of density regulation can dominate predictions for how predation will shape life history evolution (Abrams 1991, Charlesworth 1994, Abrams & Rowe 1996) and that the effects of predation can also be mediated by the way predators (or herbivores) alter the nature

of ecological interactions at lower trophic levels (e.g., Loeuille *et al.* 2002, Loeuille & Loreau 2005). While the current study does not resolve the relative importance of mortality and resource availability or direct versus indirect influences of predators on the evolution of guppy life histories, it does reaffirm that our work on life history evolution in guppies can provide a forum for studying these interactions between ecological and evolutionary processes.

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