Experimental studies of evolution in guppies: a model for understanding the evolutionary consequences of predator removal in natural communities

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Abstract

Guppies (*Poecilia reticulata*) in Trinidadian streams are found with a diversity of predators in the lower reaches of streams, but few predators in the headwaters. These differences have caused the adaptive evolution of guppy behaviour, morphology, male colouration and life history. Waterfalls often serve as barriers to the upstream distribution of predators and/or guppies. Such discontinuities make it possible to treat streams like giant test tubes by introducing guppies or predators to small segments of streams from which they were previously excluded. Such experiments enable us to document how fast evolution can occur and the fine spatial scales over which adaptation is possible. They also demonstrate that the role predators play in structuring this ecosystem resembles many others studied from a more purely ecological perspective; in these streams, as elsewhere, predators depress the numbers of individuals in prey species which in turn reduces the effects of the prey species on other trophic levels and hence the structure of the ecosystem. A focus on predators is important in conservation biology because predators are often the organisms that are most susceptible to local extinction. Their selective loss occurs because large predators have been deliberately exterminated and/or are more susceptible to environmental disturbances. Furthermore, we will argue that predator re-introductions might be destabilizing if, in the absence of predators, their prey have evolved in a fashion that makes them highly susceptible to predation, even after time intervals as short as 50–100 years. A better understanding of the evolutionary impacts of top predators will be critical goal for the policy and practice of large carnivore restoration in the future.

Keywords: carnivore, habitat restoration, *Poecilia reticulata*, predation, rewilding, top-down

Received 15 February 2007; revision accepted 4 June 2007

Introduction

A frequent consequence of the impact of humans on natural communities is the local extinction of top predators. Apex predators, such as large mammalian carnivores, are often selectively targeted because of the dangers that they pose to humans, pets, or livestock. They are also highly sensitive to habitat fragmentation because they tend to have large home ranges, low population densities, and hence low

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effective population sizes (Crooks 2002). The consequence of these attributes is that top predators are often the first species to be lost from natural communities that are being fragmented and modified by human activities. Their loss can have manifold effects on the remainder of the community. For example, we often see the rapid growth of prey populations, changes in their age structure and population dynamics, and a restructuring of the lower trophic levels (Pace *et al.* 1999). This 'keystone' effect of predators was originally described in intertidal communities, where the removal of a predator resulted in the ecological dominance of one of its prey and the consequent lost of species diversity (Paine 1974). Such effects have since been shown

in a diversity of settings including lakes, streams, tropical rainforests, temperate forests, old fields, islands and the open ocean (Mittelbach *et al.* 1995; Estes *et al.* 1998; Schmitz 1998; Crooks & Soule 1999; Pace *et al.* 1999; Berger *et al.* 2001a; Terborgh *et al.* 2001; Croll *et al.* 2005). Now, there are ongoing efforts globally to re-introduce predators where they have been lost (Noss 2001; Maehr 2001), and even discussions about reconstructing historic Pleistocene communities by restoring lost megafauna (Donlan *et al.* 2005, 2006).

We will argue, based on ongoing research on natural communities, that predators do far more than shape ecological interactions. They also can have a profound effect on the evolution of other species. Furthermore, we will show that the removal of the risk of predation can cause the rapid evolution of prey species. The nature of this evolution may result in those species being highly susceptible to predation if predators are re-introduced. The scope and speed of these evolutionary changes is such that they must be evaluated and, if necessary, accommodated if the reconstruction of predator communities is to be successful. Our intent is not to argue against re-introductions of predators — indeed we fully support such efforts — but rather to caution that restoration should be accompanied by efforts to address potential impacts on prey species and, if possible, to restore other changes that may have occurred in response to or following the initial removal of predators. We also acknowledge that what we know about the evolution and rate of evolution of prey in response to the presence or absence of predators is limited to a few study systems, largely because it has only recently been realized that evolution can be studied on short time-scales. Nevertheless, such studies represent the best available information and hence should be put to the best possible use in the design and implementation of conservation programmes.

Conservation policy is almost exclusively based on an ecological perspective of population dynamics and species interactions. This perspective implicitly assumes that the participating species do not evolve within a time frame that is relevant to conservation and management of natural resources. Our results argue that evolution is sufficiently rapid to demand that it be considered as part of policy and to alter how species conservation plans and restoration plans are implemented. To the extent that this is true, restoration must be viewed as the re-adaptation of species to a new environment and the re-ordering of ecological interactions, which may prove to be a more difficult and less predictable process than anticipated.

Introduction to the study system

Target species for conservation research do not necessarily have to be the species of immediate conservation concern.

If an organism needs to be conserved, then this means that it or its habitat is in some way threatened or endangered, which likely also implies that investigators are constrained about the sort of work that they do. Suitable subjects for establishing general principles may instead be species that are common and widespread. Although care must be taken when choosing model organisms to address conservation issues (Caro *et al.* 2005), often it is easier to study adaptation and ecology if an organism is abundant and widespread. It is also easier to study local adaptation and cause and effect relationships if the same organism is found in many environments and is amenable to experimental manipulations. We have chosen guppies on the island of Trinidad because they have these properties as an organism for field research, but also because they are ideally suited for laboratory study since they have short generation times and can be readily bred through multiple generations in a controlled environment.

Freshwater streams on the island of Trinidad represent an ideal model for evaluating the ecological and evolutionary impact of predators on their community because of the natural distribution of fish communities. Streams in the Northern Range Mountains are punctuated by waterfalls because they flow through a karst topography dissected by steep-sided ravines. The waterfalls serve as barriers to the upstream dispersal of some fish species, so that species diversity is highest in the downstream areas and becomes progressively lower upstream (Haskins *et al.* 1961; Endler 1978). There is a predictable sequence in which species are excluded in the series of waterfalls. This stair step-like structure means that we often find very different fish communities in virtually identical habitats that are immediately adjacent to one another. This pattern of distribution is repeated in a number of drainages, which yields a number of replicates of each type of community. Guppies are the focal organism of our research because they are found throughout these different communities. Finding the same fish in different settings makes them ideal subjects for looking at the effect of different environments on their ecology and evolution. We have concentrated primarily on the contrast of guppies that are found in 'high-predation communities', where they co-occur with cichlids, characins and other predators, vs. 'low-predation communities', where they co-occur with just the killifish *Rivulus hartii*. We have used mark–recapture methods to show that there are big differences in the mortality rates of guppies from high- and low-predation environments (Reznick *et al.* 1996a) (Fig. 1). When predators are absent, the probability of surviving a time interval of 200 days is around 20 times greater in a low-predation locality (Reznick & Bryant 2007).

Because of the punctuated nature of the distribution of guppies and predators, we have been able to address the
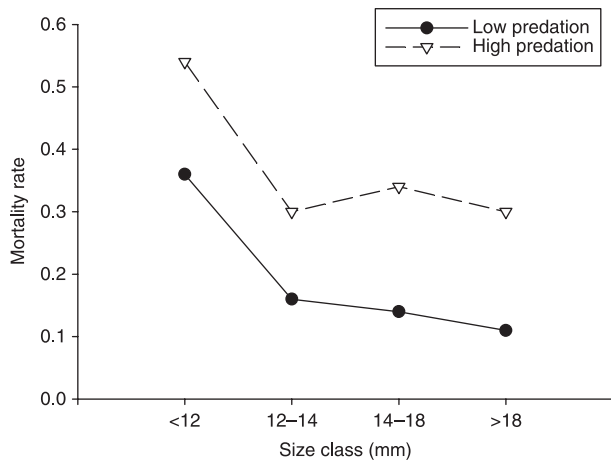
Fig. 1 Comparative mortality rates of guppies from high- and low-predation environments (modified from Reznick *et al.* 1996a). These estimates of mortality rate were derived from mark recapture studies carried out in seven high-predation and seven low-predation localities, distributed among three drainages each. The rate estimates are derived from the probability of recapture of marked fish after 12 days. These assessments included an evaluation of emigration.

impact of predators by transplanting guppies from high-predation sites over waterfalls that previously excluded all fish except the killifish. This kind of manipulation simulates the elimination of a predator. The simulation is not a perfect one because there are other differences in the fish communities associated with the presence or absence of predators. For example, some of the species that are eliminated by waterfalls may both prey on guppies and compete with them for resources. Also, the one other fish that is found above these barriers is like guppies in being far more abundant in the absence of predators. We thus use two kinds of results to support our arguments. First, we can compare many natural environments that do or do not have predators. Second, we can do experiments to see what happens to guppies as predation is either added or removed. We also note that predator removal is always accompanied by manifold effects on the community; we argue below that we see these same effects in natural populations of guppies, so the guppies, either in the context of our comparative studies or experiments, serve well as a model system for considering the effects of predator removal in other ecosystems.

We rely heavily on these introduction experiments to make inferences about the rate of evolution in such episodes of directional selection. One might question whether or not the changes that we see might also be a product of drift or founder effects. Our arguments against such alternatives are that we have replicated these intro-

ductions and get the same patterns of life-history evolution (Reznick *et al.* 1997); the patterns that we see correspond to those that we have seen in our comparative studies of a large number of natural populations (Reznick & Bryga 1996; Reznick *et al.* 1996b). If the changes in the introductions were caused by random genetic events, then they should also be random; instead, all experiments and comparative studies yield the same results. Carvalho *et al.* (1996) compared genetic variation in one of our introduction sites with the site that the colonizers were derived from and found little indication '... of stochastic forces on allozyme diversity arising from the introduction' (p. 219). On the basis of these observations, we interpret the changes in the introduction experiments as the product of natural selection.

Comparative ecology of guppies that live with and without predators

Comparative ecological studies of high- and low-predation communities revealed the same sorts of ecological correlates with the presence or absence of predators as seen in other study systems (Reznick *et al.* 2001), which suggests that the ecological effects of predators in Trinidadian streams are very much the same as elsewhere. For example, when predators are absent, population density, estimated as biomass per unit area or volume, is four to five times higher than when predators are present. In addition, individual guppy growth rates are lower and there is a shift in age structure. Both birth and death rates are lower in the absence of predators than in their presence, so the age distribution shifts from being dominated by young individuals in high-predation sites to being more uniformly distributed in low-predation sites (Rodd & Reznick 1997; Reznick *et al.* 2001) (Fig. 2). The changes that we see in guppy populations in response to the absence of predators are thus very similar to what is seen in other organisms when predators are removed from the local ecosystem (Berger *et al.* 2001a). We have seen these same shifts in population density, age structure and growth rate when guppies are transplanted from a high-predation locality to a low-predation locality, which is the equivalent of predator removal (Reznick *et al.* 2001).

Guppy evolution

We will concentrate on guppy introductions here since they characterize evolution after removal of the risk of predation. The experimental phase of our work allows us to more formally test cause-and-effect relationships. It also gives us the opportunity to consider how quickly guppies evolve when predators are removed. It has rarely been possible to measure rates of evolution as a consequence of predator removal in any natural system.
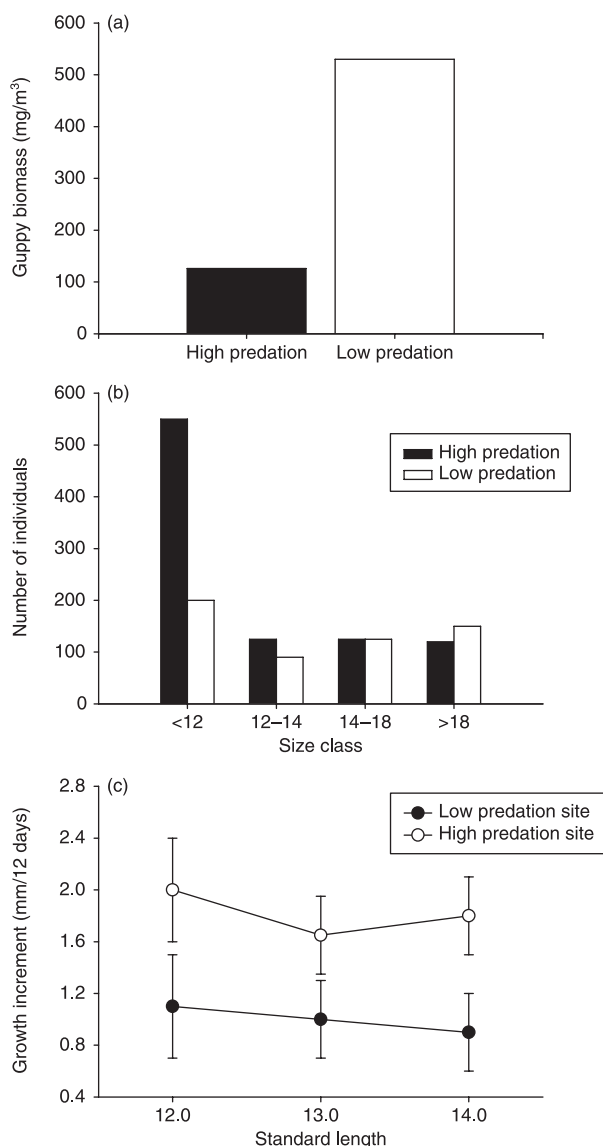
Fig. 2 Comparative population biology of guppies from high- and low-predation localities (from Reznick *et al*. 2001). These data were collected from the same 14 study sites for which we collected the mortality rate data illustrated in Fig. 1. The low-predation localities included natural low-predation environments and introduction sites. (a) Estimated biomass of guppies per unit volume of each pool. Pool volume was estimated from surface area with mapped depths. The results for mass per unit surface area are qualitatively similar. Biomass is a product of the number of guppies and their masses. The higher biomass in low-predation sites is more a function of the larger average body size of guppies than there being more guppies present. (b) Size distribution of guppies (mm): the first two size categories represent immature individuals. The third category includes all mature males and newly matured females. The largest size category includes only larger, older females. (c) Growth rates of guppies in the 12–14 mm size classes. We chose to compare these size classes because all of these fish were immature, so there would be no confounding of differences in resources invested in somatic vs. reproductive tissue.

Such rate estimates will be critical to our consideration of the relevance of our work to conservation policy.

What evolves?

Our main effort has been devoted to the quantification of life-history traits and the formal test of predictions from life-history theory. We have shown, both through comparative studies and experiments, that the added guppy mortality caused by predators selects for individuals that are younger and smaller at sexual maturity. Guppies from these localities also produce more and smaller offspring in each litter and devote more resources to reproduction than do guppies from sites without predators (Fig. 3) (Reznick & Bryga 1996; Reznick *et al*. 1996b).

Endler (1978, 1980), who was the first to fully exploit the virtues of Trinidadian streams, showed that the combined effects of predation and female preferences cause large differences among populations in male coloration. Brightly coloured males are more easily seen and targeted by predators, but are more attractive to females. When predators are present, males tend to be less brightly coloured because predators select against those that are easily seen. When predators are absent, female preferences prevail and the average male is more brightly coloured. He also showed in an experiment where he transplanted guppies from a high-predation site to a previously guppy-free low-predation site, that males will rapidly evolve brighter coloration in the absence of predators.

Guppies from high- and low-predation communities also differ in performance and behaviour. Ghalambor *et al*. (2004) showed that guppies from high-predation sites have a faster 'C-start' or 'fast start', which is a reflexive swimming response used in predator evasion (Fig. 4). Walker *et al*. (2005) found, in trials with live predators, that fish with faster C-starts are also more likely to survive an attack by a predator. Magurran *et al*. (1992) found that guppies from high-predation sites have a stronger schooling response and will not approach predators as closely as those from low-predation localities; these behaviours are believed to contribute to a defence against predators. Finally, O'Steen *et al*. (2002) found that guppies from high-predation localities have significantly higher short-term survival than those from low-predation localities when both are exposed to predators in artificial pools. This latter result does not specify why they have higher survival, but serves well as a composite measure of the consequences of all of the differences in behaviour and performance documented by earlier investigators. All of these studies included evaluations of fish that had been raised for one or more generations in a common laboratory environment in the absence of predators, so they are likely to have a genetic basis.
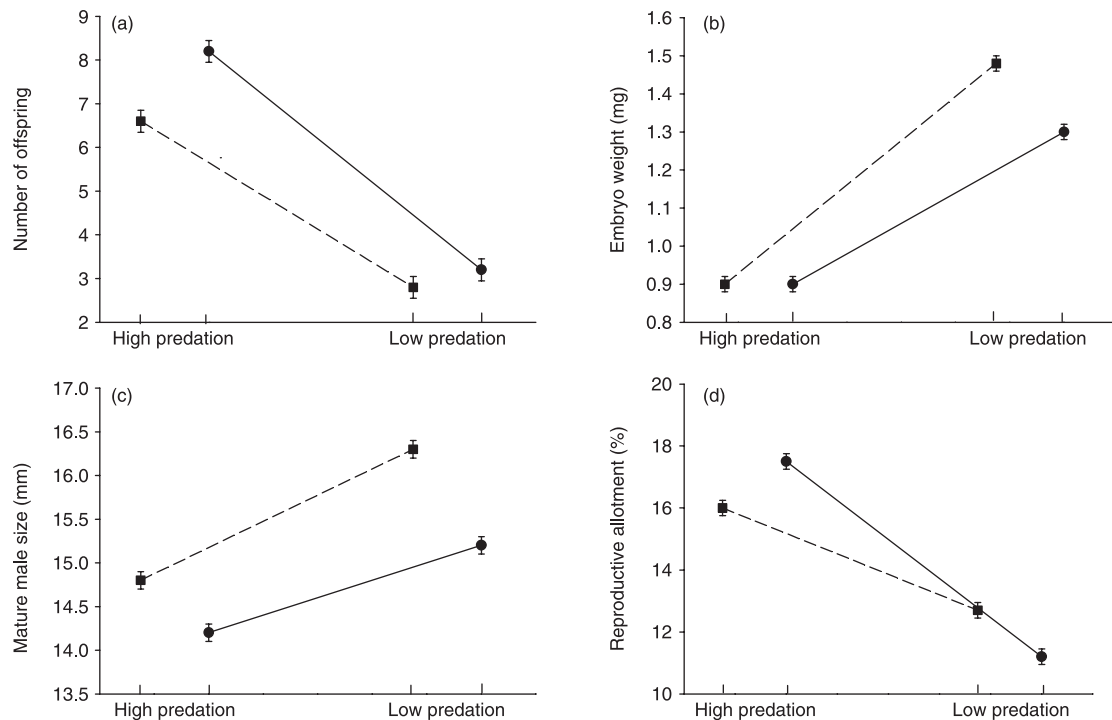
Fig. 3 (a–d from Fig. 2 in Reznick *et al*. 1996b): least-square means (± 1 standard error) of life-history traits from high- and low-predation sites on the north slope (solid line) and south slope (broken line) of the Northern Range Mountains. Each point represents an average of 5–7 populations. (a) Number of developing offspring per female, adjusted for the females somatic dry weight. (b) Dry weight of developing offspring, adjusted for their stage of development. (c) Average size of mature males. (d) Reproductive allotment of females with developing offspring, adjusted for the stage of development of the offspring.

How quickly do these traits evolve in response to a release from predation?

The key distinguishing feature of this work is that we can transplant guppies from high- to low-predation environments then quantify how quickly they evolve in response to the release from predation. Here, we will report on 'rate' just in terms of the number of years and generations associated with a given amount of change. Hendry & Kinnison (1999) present a more formal quantification of rates of evolution that includes some of these same results.

We have found that some traits evolved very rapidly, resulting in significant change in as little as 2.5 years (Table 1). The cited studies by Magurran *et al*. (1992) and O'Steen *et al*. (2002) included the evaluation of fish from the introduction experiments, so they document the evolution of these traits in response to either the removal or addition of predators. We summarize all traits that have been shown to evolve in the introduction experiments and include the time interval between when the introduction was made and the trait was evaluated in terms of years and the number of generations. There is an average of 1.74 genera-

tions per year in low-predation localities, based on data derived from our mark–recapture and life-history studies (Reznick *et al*. 1997). In many cases, the time interval associated with the evolution of a given trait represents the first time that the trait was evaluated after the introduction. For example, the behavioural assays performed by Magurran *et al*. (1992) were carried out in 1991 on fish from an introduction initiated by Caryl Haskins in 1957. This means that the trait could have evolved in less time and that this interval represents an upper bound for the time required for trait evolution. Generation time represents a common denominator that can be used to visualize how long it might take for other organisms to adapt to changes in their environment. For example, if an organism has a generation time of 5 years, then we can expect to see significant changes in traits that can influence susceptibility to predation after an absence of predators for as little as 20 or 30 years.

Predator re-introduction

Many of these changes are readily interpretable as adaptations to environments that lack predators. It is

Table 1 The number of years and number of generations required for the evolution of significant differences between guppies introduced into a predator-free environment and those from the high-predation control site that they were derived from. All traits were evaluated in individuals from the introduction and control sites that had been reared through at least two generations in a common laboratory environment then compared in a controlled laboratory setting. In these circumstances, it is very likely that any differences among populations that we see have a genetic basis since there is no confounding of environmental influences with population of origin. The number of generations was based on our estimate of 1.74 generations per year in low-predation environments (Reznick et al. 1997)

| Trait	Time interval (years)	Number of generations
Male coloration*	2.5	4.4
Male age and size at maturity†	4	7.0
Female age and size at maturity†	7.5	13.0
Offspring number and size†	11	19.1
Reproductive effort†	11	19.1
Predator escape‡	20	35.0
Schooling/predator inspection§	34	59.2

*Endler (1980).
†Reznick et al. (1987, 1990, 1997).
‡O'Steen et al. (2002).
§Magurran et al. (1992).

instructive to think of the consequences of such adaptations for that hypothetical day when predators are re-introduced. When predators are removed, guppies will evolve in a fashion that reduces potential population growth rate relative to their ancestors who were adapted to the presence of predators because they evolve later ages at maturity and produce fewer offspring. Males will be more brightly coloured and more readily seen by predators. Escape performance and other behaviours associated with predator avoidance will be less effective. All of these changes will make these guppies more susceptible to predation relative to ones from a high-predation environment. Some of these changes will be seen in as few as 2.5 years, which is around four generations. We have shown through simulations that incorporate our knowledge of guppy life histories that a population of guppies that is fully adapted to the absence of predators will go extinct if exposed to predators (Reznick et al. 2004). We have also twice transplanted guppies from a low- to high-predation site, and in both cases they failed to become established. In contrast, all five introductions of guppies from high to low predation were successful. The synthesis of these observations and simulations suggests that the re-introduction of a predator into a site from which predators have been excluded long enough to allow adaptation to
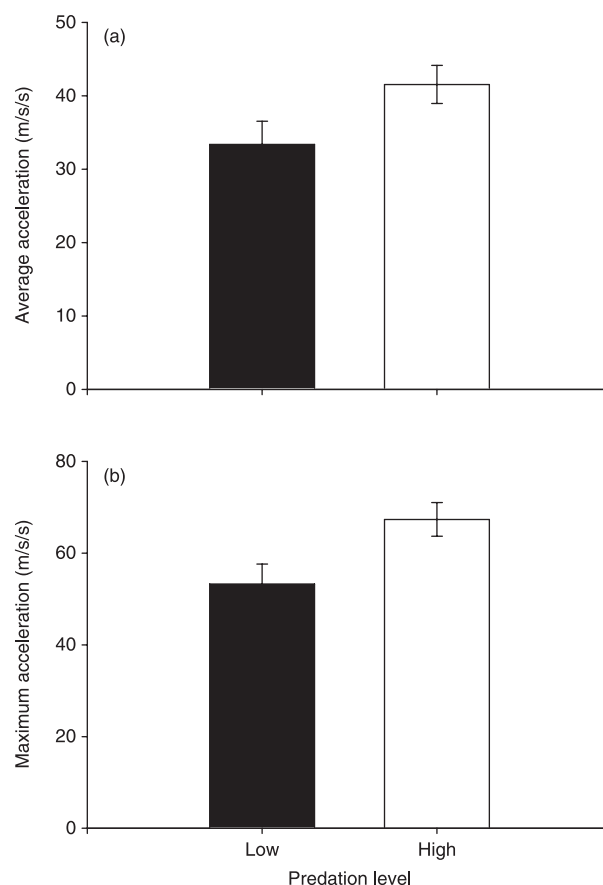
Fig. 4 (from Table 3 in Ghalambor et al. 2004): least-square means (± 1 standard error) for (a) average and (b) maximum acceleration in female guppies, adjusted for body mass. These females represent the second generation laboratory-born descendants of wild caught guppies collected from two high-predation (Oropuche and Yarra rivers) and two low-predation (Quare and Yarra Tributary) localities that represent independently derived lineages.

a low-predation environment will cause the guppies to be more susceptible to predation than guppies that have continuously lived with predators. Furthermore, this increased susceptibility could potentially cause the local extinction of guppies. These results also show that the amount of time required for these evolutionary changes to occur is relatively brief, on the order of 4–20 generations.

A dramatic example of the consequences of exposing naïve prey to new predators has been seen repeatedly when new predators are introduced to islands. For example, endemic island bird species that have evolved in the absence of predators are much more likely to go extinct than are exotic birds species when predators are introduced (Blackburn et al. 2004). This comparison is extreme because such prey have lived without predators

or without exposure to a given predator for intervals of time that are probably many orders of magnitude greater than species associated with our current conservation efforts. Yet, comparisons of animals translocated to predator-free islands from mainland sites suggest the loss of antipredator behaviour can occur over relatively short timescales (Blumstein & Daniel 2002, 2005). While these changes do not necessarily have a genetic basis, they argue that all potential prey species have had to adapt to predators in order to persist with them in their natural environment.

Are these results unique to guppies?

Investigators have now shown comparably rapid evolution in a diversity of organisms, as reviewed elsewhere by us (Reznick & Ghalambor 2001) and others (Hendry & Kinnison 1999). Examples of traits that evolve rapidly include feeding morphology and body size (Gibbs & Grant 1987), adaptation to host plant chemistry and phenology (Carroll *et al.* 1998), physiological tolerance (Lee 1999) and behaviour (Berthold *et al.* 1992). The common feature of all such studies is that they capitalize on discrete events, where there has been some sudden and dramatic change in the environment that has created an episode of intense directional selection, such as drought on the Galapagos Islands (Gibbs *et al.* 1987) or the shift of an insect to a newly introduced species of food plant (Carroll *et al.* 1998). It is this focus on discrete episodes that has given us a new perspective on the process of evolution, which is more usually thought of as something that happens very slowly and on timescales that are much longer than our lives. In the absence of such episodes, evolution may indeed be slow or may not occur at all. The kinds of change that organisms are facing in human-modified landscapes also represent episodes of directional selection, so our work is a reasonable model for the issues that confront conservation biologists who are trying to restore natural communities.

One possible example of human-induced evolution that also has relevance to conservation biology is seen in commercial fisheries (Ernande *et al.* 2004; Olsen *et al.* 2004; Hutchings 2005). Fishermen are predators that increase the mortality rate of commercially exploited fish species, often by preying selectively on the largest individuals, which are either older and/or growing more rapidly on average than the survivors. The life histories of exploited species have changed in a similar fashion to guppies over periods of a few decades. Changes include their maturing at an earlier age and smaller size. It had been thought that these changes were simply environmental in nature and that a reduction in fishing would be immediately followed by a return of these populations to their former state (Hutchings & Reynolds 2004). Instead, we see little evidence of recovery, even after many years, in populations where fishing has been reduced or completely eliminated. One possible reason is that the fish have evolved and that a consequence of this evolution is slower recovery than would be the case if the changes were just a product of phenotypic plasticity. A second possible reason is that the large-scale removal of top predators has caused a restructuring of the lower trophic levels and that something about this change in the ecosystem has slowed or prevented the rebound of the exploited species (Hutchings & Reynolds 2004).

Policy recommendations

The case study of guppies supports the conventional wisdom that naïve prey are more susceptible to predation. Why is this so? Explanations for increased susceptibility typically focus on the loss of antipredator defences without the selective force of predation. From a behavioural perspective, in the presence of top predators, prey species tend to be more secretive, foraging in secure locations and thereby maximizing survival. In contrast, in the absence of predators, prey species generally lose their defence behaviour (Terborgh *et al.* 1999; Blumstein & Daniel 2005). As highlighted above, insular ecosystems, which typically support few or no predators, provide compelling evidence for the lack of antipredator defences in the absence of predation. For example, many insular animals exhibit tame or fearless behaviour that increases their vulnerability to introduced predators, and some island birds have lost the power of flight and nest directly on the ground. Consequently, when non-native predators such as feral cats, rats, and mongoose are introduced to islands, the results can be catastrophic (Courchamp *et al.* 1999; Estes *et al.* 2001; Blackburn *et al.* 2004; Croll *et al.* 2005).

The likely failure of low-predation guppies in high-predation environments, however, could be a function of much more than changes in behaviour. Their ages at maturity and fecundity have evolved, as has male coloration and escape performance. This multifarious increase in susceptibility to predation implies that simply re-introducing predators long after the fact will not necessarily lead directly to a new, stable community. There are a few existing examples of such re-introductions and their impact on prey after absences on the order of decades to over a century. Garrott *et al.* (2005) report that the expanding population of re-introduced wolves at the headwaters of the Madison River in Yellowstone National Park have killed as much as 20% of the elk population in a single winter. Elk populations are expected to continue to decline until there is a numerical response of wolves to fewer elk (White & Garrott 2005a, b). Berger *et al.* (2001b) studied the responses of

moose to recolonzation of wolves and brown bears in Scandanavia and North America where predators have been absent for 50–130 years. Predator-naïve populations were highly vulnerable to initial encounters with predators and suffered substantial increases in the mortality of both young and adults.

These and other studies thus show that living without predators for a relatively small number of generations is sufficient for prey to become more susceptible to predation. They do not show, however, whether or not these changes are attributable to the evolution of prey. Indeed, the extent to which changes in the absence of predators are attributable to evolution will determine the rate at which prey can respond to introduced predators. Although predator-naïve prey might be initially vulnerable to re-introduced predators, if sufficient phenotypic plasticity in predator defences is present, then prey may be able to rapidly adjust to carnivore restoration. For example, although moose were highly vulnerable to initial encounters with recolonizing wolves and bears in North America, behavioural adjustments to reduce predation impacts developed within a single generation (Berger *et al*. 2001b). Specifically, Berger *et al*. (2001b) compared the responses of moose to predator auditory and olfactory cues between sites with intact predator communities and those from communities without predators. Naïve moose were significantly less responsive to such cues and sometimes behaved inappropriately by approaching the cue rather than retreating from it. Importantly though, female moose that lost offspring to predators developed exaggerated sensitivity to predator signals. The fact that at least one prey species quickly learned to be wary of restored carnivores led Berger *et al*. (2001b) to argue that restoration of carnivores will not necessarily result in localized prey extinctions. Carnivore restoration efforts, however, are as yet too recent and too few for us to know with certainty the long-term impacts of re-introduced predators on prey populations.

Similar sorts of plasticity in predator avoidance behaviour have been recorded in other predator re-introductions. Ydenberg *et al*. (2004) studied the responses of western sandpipers to the resurgence of Peregrine falcons after a 40–80 years reduction in abundance. Adults migrating north to their nesting grounds reduced their stopover time in migratory feeding grounds to reduce exposure to Peregrine Falcons. As a result, sandpipers have become progressively lighter, presumably because of reduced fat reserves, when they arrive at the breeding grounds. Gil-da-Costa *et al*. (2003) evaluated the response of howler monkeys to the re-introduction of harpy eagles on Barro Colorado Island after an absence of 50–100 years. They found that howler monkeys acquired the appropriate anti-predator behaviour in response to hearing recordings of harpy eagle calls. These examples and others have demonstrated that naïve prey can develop behaviours that reduce the risk of predation. Such behavioural plasticity may serve well as a stopgap that enables prey populations to persist in the face of predator re-introductions.

One idea that emerges from these studies is that it might it be possible to 'prime' an area for predator introduction by first exposing the local populations to nonlethal interactions with predators, or experimental 'inoculations' of small numbers of predators, to evaluate whether or not potential prey have the necessary behaviour plasticity to respond to predators. If they do, then they can begin to develop some of the appropriate defence behaviours in advance of real introductions. Such efforts might be most warranted when predator re-introductions are slated for areas supporting potential prey species that are of particular conservation concern. There is precedence for this concept of conditioning prey for the impact of predators. Because many animals in captive breeding and re-introduction programmes suffer unnaturally high levels of predation upon release, programmes will expose captive animals to predators or predator mimics to condition the captive animals with antipredator responses before release into the wild (Curio 1998).

Such priming, however, will not compensate for all of the other features of the populations that may have evolved in the absence of predators that are maladaptive in the presence of predators. In particular, life-history evolution in the prey will work against them when predators are re-introduced because low mortality rates in the absence of predators will tend to favour the evolution of delayed maturity and lower fecundity (Charlesworth 1994). Both of these life-history changes reduce potential population growth rate relative to what is possible in animals that are adapted to high mortality rates imposed by external factors, like predation. However, to the extent that prey populations display behavioural plasticity, such plasticity will reduce the initial impact of predation and increase the likelihood that prey populations persist.

A second approach is to simultaneously address any ecological changes that accompanied the earlier removal of predators. For example, it has been suggested that the local extinction of wolves and grizzly bears from parts or all of the southern Greater Yellowstone Ecosystem, in conjunction with alteration of human hunting regimes, helped to precipitate demographic eruptions and altered behaviour of moose and elk populations, followed by a restructuring of riparian plant communities (Ripple *et al*. 2001; Berger *et al*. 2001a; Ripple & Beschta 2005). Restoration efforts might reasonably address both the

re-introduction of predators and the restoration of plant communities at the same time. Of course, successful carnivore restoration also demands that conditions have improved since the carnivore species was first extirpated, and that the public is sufficiently tolerant of the re-introduced predators (Maehr 2001).

In the event that there have been extreme genetic changes in the resident population of prey during the absence of predators, there may be little that can be done to prevent the local extinction of some prey when predators are re-introduced, particularly isolated and/or rare prey populations on which predators specialize. Our failed efforts to transplant guppies from a low- to high-predation environments are an example of such a poor fit between predation and maladapted prey. The reason for such extinctions, as opposed to rapid evolution of the prey, is that the added mortality imposed by predators overwhelms the capacity of the local population to adapt to such a change. Theory has demonstrated that the capacity of a population to survive such an episode of selection will be determined more by whether or not the population can survive the initial increase in mortality rate than by whether or not it can evolve in response to selection (Gomulkiewicz & Holt 1995; Lande 1998). If the prey population is united by occasional migration with other prey populations that co-exist with the predators, then demographic rescue and interbreeding may resolve the initial imbalance caused by predator introduction. If the prey population is truly isolated, however, then restoring predators might be accompanied by the introduction of individuals derived from populations that are adapted to that predator.

It is frequently suggested that hunting by humans might replace native predators as an effective control of prey populations. In fact, the functional redundancy of human and nonhuman predators is an oft-cited justification of hunting. However, human hunters cannot always replace carnivores in an ecologically functional way because of major differences in the strategies and capabilities of human vs. carnivore hunting (Berger 2005; Ray *et al*. 2005). Moreover, 'predation' by humans is not necessarily a reasonable substitute for natural predation because of the added effects of evolution. Although both humans and predators can regulate prey density, the evolutionary impact of humans is different from predators. In one well-documented example, trophy-hunting by humans of bighorn rams appear to have reversed prior selection for large male body weight and horn size after only 30 years (Coltman *et al* 2003). A consequence of the differences in hunting styles between humans and natural predators is that they may select for different attributes in their prey. The re-introduction of natural predators into populations that have experienced human hunting, as is now being done in Western Europe and North America, may thus cause some of the same problems as re-introductions to populations that have not experienced human hunting. The same precautions should thus apply for all predator re-introductions.

Overall, a growing body of literature is increasingly revealing the varied and widespread ecological impacts of the global decline of apex predators. In contrast, although the evolutionary role of predators has been promoted as a rationale for their conservation and restoration (e.g., Maehr 2001; Noss 2001; Donlan *et al*. 2005, 2006), there has been little acknowledgement of the evolutionary consequences of their removal and hence little effort to address the special problems for prey that might accompany their re-introduction. This may be because the temporal and spatial scales necessary for the study of evolutionary processes precipitated by the extirpation or introduction of large carnivores pose a daunting challenge (Maehr 2001). The research on guppies provides a novel perspective on what these evolutionary changes might be and how fast they can occur. The history of guppy introductions to high- and low-predation environments offers some insight concerning the potential consequences to prey species of removal and re-addition of predators. We have thus given a substance and temporal frame of reference to the subject that is often lacking; the absence of such data in other systems is as likely a consequence of no one looking for it as it is of the challenge of finding it. We suggest that a better understanding of the evolutionary impacts of top predators will be critical goal for the policy and practice of large carnivore restoration in the future.

Acknowledgements

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