

Selection in Nature: Experimental Manipulations of Natural Populations¹

DAVID N. REZNICK^{2,*} AND CAMERON K. GHALAMBOR[†]

^{*}*Department of Biology, University of California, Riverside, California 92521*

[†]*Department of Biology, Colorado State University, Fort Collins, Colorado 80523*

SYNOPSIS. Numerous studies have documented evolution by natural selection in natural populations, but few are genuine selection experiments that are designed and then executed in nature. We will focus on these few cases to illustrate what can be learned from field selection experiments alone or field and laboratory selection experiments together that cannot be learned from laboratory experiments alone. Both types of study allow us to evaluate cause and effect relationships because a planned experiment can be accompanied by a more direct evaluation of the factors that cause evolution. A unique benefit of field experiments is that they give us the opportunity to measure the rate and magnitude of selection in nature. We have found that this rate is far greater than one might imagine based on observations of the fossil record. A combination of field and laboratory selection experiments has revealed the importance of population size and structure in shaping the genetics of adaptation. For example, laboratory selection experiments on insecticide resistance tend to attain resistance through polygenic inheritance. The evolution of insecticide resistance in nature often eventually yields to single genes of large effect that are rare but, once they arise, represent a higher fitness solution to resistance and spread among populations. Finally, field studies enable us to test evolutionary theory in a context in which all of the tradeoffs associated with a trait are realized; in the laboratory, organisms may be shielded from the fitness tradeoffs associated with the evolution of a trait. For example, we have compared the patterns of senescence in guppies from high and low mortality rate environments in the laboratory and in the field. In the laboratory, guppies from high predation environments had delayed senescence relative to those from low predation environments. In the field the apparent relationship is the opposite. One hypothesis for this difference is that a tradeoff associated with the evolution of the high predation life history is a decrease in the investment in the immune system. Such a sacrifice would be evident in nature where there is exposure to disease and parasites but less so in the laboratory, which is relatively disease and parasite free.

INTRODUCTION

This symposium is dominated by laboratory selection experiments. The natural reason for this pattern of representation is that virtually all selection experiments have been done in a laboratory setting. Our goal is to summarize the small number of selection experiments that have been done in nature, then to highlight what such studies can contribute to our understanding of evolution that cannot be learned from laboratory studies alone. We will argue that there is one important message derived from field experiments that can only be learned from such experiments and two messages that require a combination of field and laboratory work.

The goals of selection experiments done in a natural population are to characterize the process of evolution by natural selection and to test aspects of evolutionary theory in nature. The few such experiments that have been done share some important qualities. First, they are preceded by extensive, comparative field studies that characterize variation in the study organisms and their environments. Second, they are designed to test hypotheses that were suggested by the prior field studies and by associated evolutionary theory. Third, they

remain part of a continued interplay between experiments and field studies. Field experiments are thus embedded in larger programs of study and have designs that are inspired by these programs, rather than being stand-alone experiments.

There are only two experiments thus far that fully qualify as formal selection experiments done in nature. One was performed on guppies found in streams that drain the Northern Range Mountains of Trinidad (*e.g.*, Endler, 1980; Reznick *et al.*, 1990) and the other on *Anolis* lizards introduced to lizard-free islands in the Caribbean (*e.g.*, Schoener and Schoener, 1983; Losos *et al.*, 1997, 2001). However, there are many other studies that, while not formal field selection experiments, have also been done in a context that allow us to associate the process of adaptation with a dated event and appropriate controls and hence to make direct inferences about the process of evolution (*e.g.*, Carroll and Boyd, 1992; Grant and Grant, 2002; Hendry *et al.*, 2000; Lee, 1999). We will make use of these additional studies in our review since the information that they yield is comparable to what we have learned from formal experiments. We will first briefly review the two formal selection experiments.

The evolution of color patterns and life histories in guppies

The Northern Range Mountains of Trinidad contain a seasonal tropical rainforest that receives up to four meters of rain per year. They are well supplied with

¹ From the Symposium *Selection Experiments as a Tool in Evolutionary and Comparative Physiology: Insights into Complex Traits* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 5–9 January 2004, at New Orleans, Louisiana.

² E-mail: david.reznick@ucr.edu

streams that flow throughout the year. These streams are occupied on the south slope by a subset of the fish that characterize freshwater rivers in the Orinoco Basin in Venezuela, including cichlids and characins. The streams on the north slope contain fish that are derived from more typically marine species, including gobies and mullets. Both sets of streams have drainages that are broken up by steep, karst topography. The waterfalls that are typical of such topography often serve as upstream barriers to the dispersal of some of the larger, predatory species of fish. Guppies are distributed more widely than most other fish species, so they are frequently found co-occurring with predatory fish below barrier waterfalls and are free of such predation above such barriers. Guppies have a dramatic sexual dimorphism. Males have determinate growth, are brightly colored and their color patterns are highly polymorphic. Females have indeterminate growth, so they are generally larger than males and lack the bright pigmentation of males.

Endler (1978) found that male guppies from high predation environments have fewer, smaller color spots than their counterparts from low predation environments. He hypothesized that this pattern was caused by a balance between females preferring to mate with brightly colored males and brightly colored males being more susceptible to predation. When predators are absent, female preference results in the evolution of brighter coloration. When predators are present, they limit the effects of female preference by preying preferentially on more brightly colored males because they are also more conspicuous.

Reznick (1982) and Reznick and Endler (1982) found that the presence of predators was also associated with guppies that attained maturity at an earlier age and reproduced more frequently. They had more offspring in each litter, the size of individual offspring was smaller, and the quantity of consumed resources that was devoted to reproduction was larger than in guppies from low predation localities. These patterns were shown to have a genetic basis because they persisted in the second generation of lab-born guppies that were reared on controlled levels of food availability. We hypothesized that these patterns were caused by the differences in mortality rate between high and low predation localities. Specifically, we hypothesized that guppies from high predation environments sustain higher adult mortality rates because many of the predators were known to prey preferentially on the larger size classes. In contrast, guppies from low predation localities should experience selective predation on immature size classes because the one fish predator found there, *Rivulus hartii*, is gape limited and preys primarily on the smaller size classes. The hypothesized association between mortality and life histories was based on predictions from life history theory (e.g., Charlesworth, 1980; Gadgil and Bossert, 1970; Law, 1979; Michod, 1979). We later directly estimated mortality rates with mark-recapture studies (Reznick *et al.*,

1996) and showed that these general patterns were obtained.

Both of these studies demonstrate that the patterns in male coloration and life histories are found across a diversity of streams from throughout the Northern Range Mountains (see also Reznick *et al.*, 1996a; Reznick and Bryga, 1996). There are thus many replicate streams which show the same patterns and provide the raw material for subsequent experiments. Both studies also reveal that differences between high and low predation environments can be seen over very small distances, such as in samples collected only tens of meters apart from above and below barrier waterfalls that serve to prevent upstream dispersal of predators (Endler, 1978; Reznick and Endler, 1982). Since such sites are identical in all regards, except for the presence or absence of predators, it seems likely that predators are responsible for the observed differences.

The actual experiments exploited the discontinuities in the distribution of guppies and guppy predators caused by barrier waterfalls and treated streams as if they were giant test tubes. In two cases, we found streams that had a waterfall that served as a barrier to all species of fish except *R. hartii*. This fish has superior dispersal capabilities, because it is able to leave streams on rainy nights, hop across the forest floor, and disperse to ephemeral pools and portions of streams above barrier waterfalls. We thus often find streams above dramatic waterfalls that only contain *R. hartii*. In both cases, we collected guppies from the high predation site below the barrier waterfall and introduced them into the previously guppy-free low predation site above the barrier waterfall. We consider the descendants of the introduced guppies to be our experimental treatment and use those from the high predation site below the barrier waterfall as a control. Inferences about the evolution of male coloration or life history traits are based on a comparison of experimental and control guppies.

A second type of experiment involved a barrier waterfall on the Aripo River. This barrier represented the upstream limit for a suite of larger predators, but not for guppies, *R. hartii*, and a few other species of fish. Here we collected predators from below the barrier and introduced them over the barrier. Their subsequent upstream dispersal was limited by the presence of another barrier waterfall shortly upstream. This experimental treatment increased the mortality rate of the affected guppies. Their evolution was evaluated with respect to control guppies collected from the high predation site below the barrier waterfall and others collected from the low predation site upstream of the secondary barrier waterfall.

Together we have two experiments in which guppy mortality rates were either reduced or increased in the field. With regard to male coloration, Endler predicted that the release from predation would result in the predominance of female preferences for brightly colored males and hence the evolution of males with larger spots in the introduction site in comparison to the high

predation control. This prediction has only been evaluated in one of the two experiments in which guppies were moved from a high to a low predation locality. Males from the introduction site had significantly larger spots than those from the control site, only two years after the introduction (Endler, 1980). In the case of life history traits, the goal was to test a particular facet of life history theory in nature. Transplanting guppies from a high to a low predation environment was predicted to select for individuals that attain maturity at a later age and have a lower rate of investment in reproduction. We also expected them to produce fewer, larger offspring than their counterparts from the high predation control. Transplanting predators to a low predation site was predicted to select for individuals that have an earlier age at maturity relative to controls found above the secondary barrier waterfall. All of these predictions were upheld. In one of the replicate introductions of guppies from a high to low predation site, male age and size at maturity had evolved in the predicted direction within four years (Reznick and Bryga, 1987), and female age and size at maturity changed as predicted within seven years (Reznick *et al.*, 1990). In the second introduction of guppies from a high to low predation site, male age and size at maturity, female age and size at maturity, reproductive effort, offspring size, and offspring number had all changed as predicted within 11 years (Reznick *et al.*, 1990). When mortality rate was increased by adding predators, the age at maturity of males and females both decreased relative to the low predation control after five years (Reznick, 1997).

In all of these studies the genetic basis of differences between high and low predation sites has been evaluated by rearing guppies in a common laboratory environment for at least two generations. Such “common garden” experiments remove or greatly reduce variation due to environmental or maternal effects and provide evidence on whether genetic change has occurred between populations.

The evolution of limb morphology in Anolis lizards

The second example of selection experiments done in nature was executed by Tom Schoener, Jonathan Losos and colleagues on *Anolis* lizards. This research was preceded by extensive studies of the distribution and adaptive radiation of *Anolis* lizards in the Caribbean (*e.g.*, Williams, 1972, 1983; Schoener and Schoener, 1983; Losos, 1994; Losos *et al.*, 1994, 1997, 1998, 2001). Earlier studies had found that each of the islands making up the Greater Antilles has a similar assemblage of *Anolis* lizards that are specialized for particular habitats and lifestyles, termed “ecomorphs” (Williams, 1972, 1983). For example, a number of islands have ecomorphs referred to as crown giants, which are large species that live in tree canopies. Other ecomorphs include twig specialists that are small, short-legged species that tend to be found on branches of small diameter, and trunk-crown specialists, which have well-developed toe pads and elongated bodies

that tend to be found on tree trunks and branches from eye level to high in the tree (*e.g.*, Losos, 1994; Losos *et al.*, 1994). Laboratory and field studies confirmed that these relationships between morphology and habitat have an adaptive basis with respect to locomotor performance (Irschick and Losos, 1998, 1999). DNA-based phylogenies demonstrated that similar adaptive radiations have occurred independently and repeatedly on different islands. For example, trunk-crown anoles tend to be more closely related to *Anolis* species on the same island with different body shapes and ecological specializations than they are to trunk-crown anoles on other islands (Losos *et al.*, 1998). These associations between habitat preference, morphology, and performance suggest that these differences in morphology evolved independently and repeatedly as adaptations to specific environmental conditions rather than evolving once and spreading through dispersal. If the interspecific and interpopulation differences in limb morphology represent locomotor adaptations to specific types of vegetation and habitats, then populations that have adapted to islands with different structured communities should evolve similar differences in limb morphology as seen in natural populations.

In 1977 and 1981, *Anolis sagrei* from a common source population was introduced to 14 previously lizard-free islands in the Bahamas. These islands varied in the type of vegetation that they had, yielding predictions for how limb morphology should evolve as each new population adapted to its island. Losos *et al.* (1997) found a significant association between morphology and vegetation structure after a time interval of 10–14 years. It remains to be seen whether or not these differences are a function of phenotypic plasticity or changes in the genetic composition of the population (Losos *et al.*, 2001). However, based on these results it is clear that the potential for relatively rapid adaptive differentiation in nature is possible. This rapid adaptive differentiation is also seen in the most recent set of experiments. Previous work has shown that on islands where the predatory and ground-dwelling curly-tailed lizard (*Leiocephalus carinatus*) is present, populations of *A. sagrei* shift habitat use by moving higher up in the vegetation (Losos, 1994). In 2003, *L. carinatus* was introduced to six small islands in the Bahamas resulting in a rapid adaptive behavioral shift in habitat use in response to the new predator-induced selection pressures (Losos *et al.*, 2004). Such experiments represent some of the first attempts to test the role of behavior and other phenotypically plastic traits driving adaptive evolution in nature and may provide considerable insight into mechanisms responsible for rapid evolutionary changes (Losos *et al.*, 2004).

Field studies of guppies and *Anolis* lizards share key properties. Both use extensive prior field studies to evaluate patterns and develop hypotheses within a framework that allows for the formulation of *a priori* predictions. Both use manipulations that mimic events that frequently occur in nature. For example, the in-

roduction of lizards mimics the continuous natural colonization (and often subsequent extinction) of these islands by lizards (*e.g.*, Losos *et al.*, 2001). Both test these hypotheses with manipulations of natural populations in a field setting. Both yield direct inferences about the process of evolution by natural selection. Finally, both studies are on-going and dynamic as results from previous observations and experiments inform future experiments.

While there are few formal experiments done in nature, there are a much larger number of studies that document evolution and adaptation in a context in which there is some history and hence information that is a close equivalent to a designed experiment, such as the accidental introduction of species into new environments (see Reznick and Ghalambor, 2001). We will use some examples of this sort of work to illustrate our points. Some important examples include: the characterization of how soapberry bugs (*Jadera haematoloma*) adapt to new, exotic plant hosts that were introduced into the bug's range at approximately known times (Carroll and Boyd, 1992); the adaptation of marine rotifers that have recently invaded freshwater environments (Lee, 1999; Lee and Bell, 1999); and the adaptation of yucca moths that exploit a new species of host (Groman and Pellmyr, 2000). These and many more studies contain excellent analyses of adaptation to a new environment that can be associated with some historical change in the environment. All of them reveal information about responses to selection that is comparable to what has been learned from the two available field selection experiments.

Lesson 1: what unique knowledge can be derived from selection experiments in nature?

A key piece of information revealed by these contemporary studies of adaptation that cannot be obtained in laboratory selection experiments is that they yield estimates of the potential rate of evolution in nature. These studies consistently reveal that the rate of evolution seen in contemporary studies can be many orders of magnitude faster than rates that are inferred from the fossil record. Stearns (1992), for example, updated Gingerich's (1983) comparisons of rates of evolution estimated from fossils, historical introductions, and artificial selection to include estimates of rates derived from the guppy introduction experiments. The seemingly small changes found in guppies were associated with rates of evolution that were of the same order of magnitude attained by artificial selection and four to seven orders of magnitude higher than seen in the fossil record. Virtually all of the other contemporary studies of evolution reveal similar results (see Hendry and Kinnison, 1999).

These results bear three important messages. The first message is that our perceptions of the rate of evolution that are based on the fossil record and that have played an important historical role in shaping our impressions of what evolution is like, are strongly biased and systematically underestimate the true potential rate

of evolution. This bias occurs because inferences from the fossil record are based on long term averages that are likely to include long intervals of no change or reversals in the direction of change. The second message is that it might be more accurate to think of evolution as a series of relatively rapid, discrete events rather than prolonged, continuous change. Evolutionary trends, such as the fossil record, are an epiphenomenon of average long-term trends in these many discrete events. The third message is that the reason that evolution is not usually seen is not because it is too slow, as Darwin assumed, but because it is too fast. Evolution may well be concentrated in small, brief events and will only be seen if it is looked for, such as in the context of an experiment or as part of an individual mark-recapture study that is associated with the quantification of individual traits, as in work on Galapagos finches (Grant and Grant, 1995) or side-blotched lizards (Sinervo and Lively, 1996; Sinervo *et al.*, 2000), or in association with a cause that has a known time reference, as with the soapberry bugs.

There are two additional lessons that can be inferred from a combination of laboratory and field work.

Lesson 2: what is the importance of population structure?

Through the combination of the laboratory and field selection we also learn something about the importance of population structure and size. Lab selection imposes a specific population structure, meaning that investigators begin with a population of a given size and there is generally no continuing influx of new genes through migration. When selection occurs in nature, it will often play out in the context of a metapopulation, or many semi-isolated populations that are joined by gene flow. Thus, under natural conditions gene flow between populations can either oppose the fixation of beneficial alleles within a local population (*e.g.*, Slatkin, 1987) or facilitate the spread of alleles that confer a fitness advantage (*e.g.*, Lenormand *et al.*, 1998).

The evolution of insecticide resistance in insects has been evaluated multiple times in the lab and field and hence serves as a good example of the differences between the two selective environments. When selection was done on lab lines for insecticide resistance, the genetic basis for the evolution of resistance is caused by whatever polygenic variation was available in the founder population and resistance often involves many alleles of small effect (*e.g.*, McKenzie and Batterham, 1994). However, in nature resistance evolves through the substitution of single genes of large effect which can appear as rare mutations and spread through migration, in part because of the large number of semi-isolated populations exposed to selection and connected by long distance dispersal (*e.g.*, Lenormand *et al.*, 1998; Chevillon *et al.*, 1999). Assays of resistance in the field thus tend to reveal that it is caused by one or few genes of large effect (McKenzie and Batterham, 1994). In this case, the discrepancy between laboratory

and field assays may arise because laboratory lines are initiated from a small to moderate number of field collected individuals that may lack rare alleles that have large effects on resistance (Roush and McKenzie, 1987). The bottom line is that lab selection can focus on a biased subset of the genetic mechanisms that cause a trait to evolve.

Lesson 3: how important are trade-offs among fitness traits in shaping the response to selection?

Our perception of the relative importance of trade-offs among fitness traits can often be a function of the environment in which these trade-offs are evaluated (Reznick *et al.*, 2000). The differences among populations in the laboratory and field can be strongly affected by such a context-specific effect of trade-offs, often because organisms can be shielded from trade-offs in the lab that might have a large impact in nature. For example, the same alleles conferring resistance and a fitness benefit in the presence of insecticides impose a fitness cost in the absence of insecticides (Chevillon *et al.*, 1999; Bourguet *et al.*, 2004). Such important pleiotropic effects are only revealed in the context of heterogeneous environments and comparative studies of populations, or conditions more likely to be observed under field rather than laboratory conditions. Our studies of senescence in guppies from high and low predation environments in the lab *versus* the field illustrate another possible example of the context-specific nature of tradeoffs.

Evolutionary theory predicts that high predation environments, where we have seen the evolution of earlier maturity and increased reproductive investment, will also select for an earlier onset of senescence and shorter lifespan (Medawar, 1952; Williams, 1957). Senescence in nature can be detected as an acceleration in mortality rate in older age groups. We tested this prediction in two contexts. First, we estimated the mortality rate of guppies in a natural low predation environment in comparison with an introduction experiment in which high predation guppies had been introduced into a low predation environment. Here we predicted that the introduced guppies, which now had the opportunity to live well beyond what their lifespan would be in the presence of predators, would have earlier senescence than the natural low predation population. Earlier senescence means that this acceleration in mortality rate should be detectable at an earlier age and may perhaps be more rapid in the introduced guppies relative to the natural low predation guppies.

As predicted, we found that high predation guppies had higher mortality rates overall and an earlier onset of an acceleration in mortality rate relative to low predation guppies (Bryant and Reznick, 2004). This observation is unreplicated and is subject to alternative interpretations, but it is at least consistent with the prediction that higher extrinsic mortality rates, meaning mortality that is attributable to external causes such as predation, will also select for earlier senescence. We also tested this hypothesis in the laboratory, this time

by comparing the grandchildren of wild-caught females from two high and two low predation localities. These localities represent two different drainages, each of which was represented by a high and low predation population. Prior genetic work argues that the differences in life history between high and low predation sites evolved independently in each drainage (Carvalho *et al.*, 1991; Fajen and Breden, 1992), so the two drainages represent genuine duplicates of life history evolution. We found in both replicates, and in an earlier pilot study, that the guppies from high predation environments have deferred senescence relative to those from low mortality rate environments. The delayed senescence in high predation guppies is evident in their showing an acceleration of mortality rate at a later age, having longer average total lifespans, longer reproductive lifespans, and higher fecundity throughout their lives (Reznick *et al.*, 2004). These laboratory results are thus the opposite of predictions derived from evolutionary theory.

Why would we find opposite results in the laboratory and the field? In the field mark-recapture assay, high predation guppies transplanted to a low predation environment had an earlier onset of senescence than the native low predation environment. In the laboratory, guppies derived from two high predation localities had delayed senescence in comparison to counterparts from low predation localities in the same drainage. One general explanation for the difference is that there is an important but unmeasured fitness trade-off associated with these life history traits that has a strong affect on natural populations but not on laboratory populations. One such trade-off could be the immune system. The immune system is costly to maintain and may be included in the complex of trade-offs associated with the evolution of life history traits (*e.g.*, Sheldon and Verhulst, 1996; Lochmiller and Deerenberg, 2000; Norris and Evans, 2000). For example, high predation guppies may be able to invest more in growth and reproduction early in life because they invest less in the immune system. In a natural high predation locality, they may well not live long enough to pay a price for this savings. In the laboratory, they are generally shielded from disease and parasites, so they will not pay this price, while in the field there will be a constant risk of exposure to disease. When high predation guppies are introduced into a low predation environment and have the opportunity to live longer, this trade-off may then become more apparent. It happens that the guppies in our introduction site did experience a high frequency of what appeared to be a bacterial infection. Such an infection is likely to have played a role in their higher mortality rate and earlier acceleration in mortality. It may also be the manifestation of such a trade-off between investment in growth and reproduction *versus* investment in the immune system. Whether or not this particular tradeoff accounts for the differences observed between our laboratory and field studies remains to be seen. It at least serves as a hypothesis for how such differences between the labo-

ratory and field could arise and illustrates the added value of evaluating the consequences of selection in multiple environments. Similar conclusions have emerged from the comparisons of lifespans in laboratory strains *versus* wild strains of *Caenorhabditis elegans* (Walker *et al.*, 2000), *Mus musculus* (Miller *et al.*, 2002), or *Drosophila melanogaster* (Linnen *et al.*, 2001).

SUMMARY AND CONCLUSIONS

Selection experiments can be done on natural populations. They reveal that adaptive evolution can be much more rapid than previously thought and open up the possibility of complimenting laboratory selection experiments with studies of natural populations. This conclusion is reinforced by a much larger number of non-experimental studies of adaptation that are linked to a time reference and hence allow us to make inferences about the rate of evolution and show that this inference of a high potential rate of evolution is obtainable in a diversity of organisms. A combination of evaluations of selection in the field and laboratory also reveals that population size and structure can affect the outcome and genetic basis of selection. Because the laboratory imposes a specific population size and structure that most often does not relate well to natural populations, the kind of response seen in the laboratory may also fail to represent how organisms are likely to evolve in the field. The repeatability of adaptive evolution at the phenotypic level in response to specific selection pressures has already been demonstrated under both field (*e.g.*, Reznick *et al.* 1996a; Losos *et al.*, 1997) and laboratory (*e.g.*, Rainey and Travisano, 1998; Travisano and Rainey, 2000) conditions. However, much remains to be learned about the repeatability of the underlying genetic architecture of these events. Future studies that specifically evaluate factors such as population size and structure under laboratory and field conditions could provide insight into this largely unexplored area of research. Finally, a combination of laboratory and field work reveals that studying organisms in the laboratory alone often means studying evolution in the absence of trade-offs that are normally present in nature. These trade-offs arise because organisms in nature typically occur within a mosaic of heterogeneous environments and under a diversity of selection pressures. Thus, pleiotropic effects and other fitness costs associated with alleles that would otherwise be favored in response to a given form of selection suggest that the absence of any fitness tradeoffs can yield a diversity of laboratory artifacts. In summary, we argue that our understanding of how phenotypes and genotypes respond to selection will be better informed by studies of adaptation in both laboratory and natural conditions.

REFERENCES

- Bourguet, D., T. Guillemaud, C. Chevillon, and M. Raymond. 2004. Fitness costs of insecticide resistance in natural breeding sites of the mosquito *Culex pipiens*. *Evolution* 58:128–135.
- Bryant, M. and D. Reznick. 2004. Comparative studies of senescence in natural populations of guppies. *Am. Nat.* 163:55–68.
- Carroll, S. B. and C. Boyd. 1992. Host race radiation in the soapberry bug: Natural history with the history. *Evolution* 46:1052–1069.
- Carvalho, G. R., P. W. Shaw, A. E. Magurran, and B. H. Seghers. 1991. Marked genetic divergence revealed by allozymes among populations of the guppy *Poecilia reticulata* (Poeciliidae), in Trinidad. *Biol. J. Linn. Soc.* 42:389–405.
- Charlesworth, B. 1980. *Evolution in age structured populations*. Cambridge University Press, Cambridge, U.K.
- Chevillon, C., M. Raymond, T. Guillemaud, T. Lenormand, and N. Pastuer. 1999. Population genetics of insecticide resistance in the mosquito *Culex pipiens*. *Biol. J. Linn. Soc.* 68:147–157.
- Endler, J. A. 1978. A predator's view of animal color patterns. *Evol. Biol.* 11:319–364.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91.
- Fajen, A. and F. Breden. 1992. Mitochondrial DNA sequence variation among natural populations of the Trinidad guppy, *Poecilia reticulata*. *Evolution* 46:1457–1465.
- Gadgil, M. and P. W. Bossert. 1970. Life historical consequences of natural selection. *Am. Nat.* 104:1–24.
- Gingerich, P. D. 1983. Rates of evolution: Effects of time and temporal scaling. *Science* 222:159–161.
- Grant, P. R. and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49:241–251.
- Grant, P. R. and B. R. Grant. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296:707–711.
- Groman, J. D. and O. Pellmyr. 2000. Rapid evolution and specialization following host colonization in a yucca moth. *J. Evol. Biol.* 13:223–236.
- Hendry, A. P. and M. T. Kinnison. 1999. The pace of modern life: Measuring rates of contemporary microevolution. *Evolution* 53:1637–1653.
- Hendry, A. P., J. K. Wenburg, P. Bentzen, E. C. Volk, and T. P. Quinn. 2000. Rapid evolution of reproductive isolation in the wild: Evidence from introduced salmon. *Science* 290:516–518.
- Irschick, D. J. and J. B. Losos. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* 52:219–226.
- Irschick, D. J. and J. B. Losos. 1999. Do lizards avoid habitats in which performance is submaximal? The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* 154:293–305.
- Law, R. 1979. Optimal life histories under age-specific predation. *Am. Nat.* 114:399–417.
- Lee, C. E. 1999. Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution* 53:1423–1434.
- Lee, C. E. and M. A. Bell. 1999. Causes and consequences of recent freshwater invasions by saltwater animals. *Trends Ecol. Evol.* 14:284–288.
- Lenormand, T., T. Guillemaud, D. Bourguet, and M. Raymond. 1998. Appearance and sweep of a gene amplification: Adaptive response and potential for new functions in the mosquito *Culex pipiens*. *Evolution* 52:1705–1712.
- Linnen, C., M. Tatar, and D. E. L. Promislow. 2001. Cultural artifacts: A comparison of senescence in natural, laboratory-adapted and artificially selected lines of *Drosophila melanogaster*. *Evol. Ecol. Res.* 3:877–888.
- Lochmiller, R. and C. Deerenberg. 2000. Trade-offs in evolutionary immunology: Just what is the cost of immunity? *Oikos* 88:87–98.
- Losos, J. B. 1994. Integrative studies of evolutionary ecology: Caribbean *Anolis* lizards as a model system. *Ann. Rev. Ecol. Syst.* 25:467–493.
- Losos, J. B., D. J. Irschick, and T. W. Schoener. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution* 48:1786–1798.
- Losos, J. B., T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodriguez-Schettino. 1998. Historical contingency and determinism

- in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118.
- Losos, J. B., T. W. Schoener, and D. A. Spiller. 2004. Predator-induced behaviour shifts and natural selection in field experimental lizard populations. *Nature* 432:505–508.
- Losos, J. B., T. W. Schoener, K. I. Warheit, and D. Creer. 2001. Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards. *Genetica* 112–113:399–415.
- Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* 387:70–73.
- McKenzie, J. A. and P. Batterham. 1994. The genetic, molecular and phenotypic consequences of selection for insecticide resistance. *Trends Ecol. Evol.* 9:166–169.
- Medawar, P. B. 1952. *An unsolved problem of biology*. H. K. Lewis and Co. Ltd., London, U.K.
- Michod, R. E. 1979. Evolution of life histories in response to age-specific mortality factors. *Am. Nat.* 113:531–550.
- Miller, R. A., J. M. Harper, R. C. Dysko, S. J. Durkee, and S. N. Austad. 2002. Longer life spans and delayed maturation in wild-derived mice. *Exp. Biol. Med.* 227:500–508.
- Norris, K. and M. Evans. 2000. Ecological immunology: Life history trade-offs and immune defense in birds. *Behav. Ecol.* 11:19–26.
- Rainey, P. B. and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. *Nature* 394:69–72.
- Reznick, D. N. 1982. The impact of predation on life history evolution in Trinidadian guppies: The genetic components of observed life history differences. *Evolution* 36:1236–1250.
- Reznick, D. N., M. J. Butler IV, F. H. Rodd, and P. Ross. 1996. Life history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution* 50: 1651–1660.
- Reznick, D. N. 1997. Life history evolution in guppies (*Poecilia reticulata*): Guppies as a model for studying the evolutionary biology of aging. *Exp. Geront.* 32:245–258.
- Reznick, D. N., M. J. Bryant, D. Roff, C. K. Ghalambor, and D. E. Ghalambor. 2004. Effect of extrinsic mortality on the evolution of senescence in guppies. *Nature* 431:1095–1099.
- Reznick, D. N. and H. Bryga. 1987. Life-history evolution in guppies. 1. Phenotypic and genotypic changes in an introduction experiment. *Evolution* 41:1370–1385.
- Reznick, D. N. and H. Bryga. 1996. Life-history evolution in guppies (*Poecilia reticulata*: Poeciliidae). V. Genetic basis of parallelism in life histories. *Am. Nat.* 147:339–359.
- Reznick, D. N., H. Bryga, and J. A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- Reznick, D. N., M. J. Butler, F. H. Rodd, and P. Ross. 1996b. Life history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution* 50: 1651–1660.
- Reznick, D. N. and J. A. Endler. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* 36:160–177.
- Reznick, D. N. and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: What empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112–113:183–198.
- Reznick, D. N., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends Ecol. Evol.* 15:421–425.
- Reznick, D. N., F. H. Rodd, and M. Cardenas. 1996a. Life history evolution in guppies (*Poecilia reticulata*). IV. Parallelism in life-history phenotypes. *Am. Nat.* 147:319–338.
- Roush, R. T. and J. A. McKenzie. 1987. Ecological studies of insecticide and acaricide resistance. *Ann. Rev. Entomol.* 32:361–380.
- Schoener, T. W. and A. Schoener. 1983. Time to extinction of colonizing propagule of lizards increases with island size and avifaunal richness. *Nature* 274:685–687.
- Sheldon, B. and S. Verhulst. 1996. Ecological immunology: Costly parasite defenses and trade-offs in evolutionary ecology. *Trends Ecol. Evol.* 11:317–321.
- Sinervo, B. and C. M. Lively. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380: 240–243.
- Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. *Nature* 406:985–988.
- Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787–792.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford, U.K.
- Travisano, M. and P. B. Rainey. 2000. Studies of adaptive radiation using model microbial systems. *Am. Nat.* 156:S35–S44.
- Walker, D. W., G. McColl, N. L. Jenkins, J. Harris, and G. J. Lithgow. 2000. Evolution of lifespan in *C. elegans*. *Nature* 405:296–297.
- Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: A trial analysis. *Evol. Biol.* 6:47–89.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: Studies of a model organism*, pp. 326–370. Harvard Univ. Press, Cambridge, Massachusetts.
- Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. *Evolution* 11:398–411.