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## FIELD EXPERIMENTS, INTRODUCTIONS, AND EXPERIMENTAL EVOLUTION

*A Review and Practical Guide*

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The field of evolutionary biology has primarily adopted a descriptive approach throughout its history, in large part due to the difficulty of replicating evolutionary processes under controlled conditions. However, experimental approaches provide a powerful tool kit for researchers to disentangle cause and effect (Hurlbert 1984; Futuyma and Bennett this volume; Huey and Rosenzweig this volume). In the context of evolution, experimental approaches are especially attractive because of the potential for replicating rarely observed evolutionary forces, such as natural selection, drift, or the occurrence of movement into a novel environment (Garland and Kelly 2006). Laboratory experimental approaches to evolution have long been fashionable (e.g., this volume; Bradley et al. 1999; Teotónio et al. 2004), and manipulative studies have often been used for testing ideas about adaptation (Sinervo and Basolo 1996; Travis and Reznick 1998). In this vein, field experiments offer a complementary opportunity for addressing evolutionary questions in more natural circumstances (Reznick and Ghalambor 2005). Field experiments come in different forms, but the most widely discussed method in the context of evolution is field introduction of live animals, either intentional or unintentional (Reznick and Ghalambor 2005; Strauss et al. 2006). Moreover, field experiments examining evolution are likely to rise in popularity as researchers become increasingly aware that species can rapidly evolve to novel environments in an era of dramatic climate change (Carroll et al. 2007).

Within the broader context of experimental evolution, field introductions play an interesting role for several reasons. First and foremost, field introductions represent an ecological point of comparison for laboratory studies that artificially manipulate population dynamics. As the breadth of this volume shows, laboratory studies of experimental evolution are diverse and widespread. However, no laboratory experiment, no matter how complex, can replicate the structure of natural surroundings or the balance of different types of selection and trade-offs that characterize natural settings. Long-term studies of adaptation in nature invariably reveal that adaptation represents a compromise among diverse forms of selection (Reznick and Travis 1996). In laboratory settings, trade-offs between traits are often absent or weakened, and therefore potential constraints on evolution are often relaxed. In nature, strong trade-offs can act as a strong constraint on evolutionary change, and understanding the nature of this constraint is essential for predicting evolutionary responses to environmental perturbations. On the other hand, any field study presents its own set of issues that must be overcome; for example, the complexity of field settings can be problematic when attempting to discern cause and effect because of the large number of uncontrolled variables. A key point of this review is to discuss ways that researchers can cope with this seemingly overwhelming complexity.

Our goal is to provide a practical guide for researchers interested in experimental evolution and field introductions. We do not comprehensively review the topic of field introductions, as other essays have recently reviewed the topic of experimental field manipulations (Reznick and Ghalambor 2005) and the evolutionary consequences of introduced species (e.g., invasive species, Strauss et al. 2006). We begin by differentiating

different kinds of field “experiments” in regard to the study of evolution, and we discuss specific considerations for these different kinds of studies. We also provide brief encapsulations of well-known examples of field introductions that provide an overview of the range of possible study methods that researchers can access.

We define two classes of experiments. We first discuss what we term “replacement” experimental methods, which employ fake (replica) organisms that are then assessed for environmental effects (e.g., predator bites). We believe that such methods are underappreciated as part of the experimental study of evolution, but we argue that they play an essential role for understanding of how selection operates. The second class of methods is the introduction of live organisms into novel habitats. Strictly speaking, experimental approaches entail purposeful manipulation. By this definition, field experiments that manipulate the environment and then examine the evolution of target organisms in response to the manipulation are rare (Reznick and Ghalambor 2005). However, if one relaxes this definition, one can also effectively use a wider range of “manipulations” as examples of experimental evolution, even if they are not the product of planned experiments.

Within this second class, we distinguish between “human-planned” and “unplanned natural” introductions. “Human-planned” introductions represent rare and intentionally designed field experiments, such as those conducted by Reznick et al. (1990) and Losos et al. (1997). “Unplanned natural” introductions represent the other extreme, such as in the case of invasive species or the intentional human introductions of species for biological control, and so forth. We note that these latter introductions are “intentional” but to a large extent unplanned, as there is typically little forethought as to the number of colonizing individuals or to the collateral impact of these individuals to different components of the ecosystem. Besides examining each of these categories and discussing their advantages and disadvantages, in the second part of the chapter we address the unique advantages of field introductions for addressing evolutionary issues.

## **METHODS FOR FIELD MANIPULATIONS**

### **REPLACEMENT METHODS**

#### *BACKGROUND*

These methods probe how selection operates in a natural setting and enable one to make inferences about how and why certain features of organisms have evolved. Replacement methods consist of placing synthetic replicas of real organisms in the natural environment, primarily to quantify the impact of predation. Replacement methods offer an interesting and underutilized method for assessing the strength of natural selection on natural populations. Because replica models are not living organisms, one cannot typically study how predation causes evolutionary change, and thus, these methods stand apart from the other field experiments noted here. Despite this shortfall, these methods are unparalleled for studying the impact of predation, which is perhaps the most powerful selective

force in nature, on natural populations. Natural predation events are infrequently observed, and replacement methods enable researchers to study predation in a quantitative context, as opposed to the rare (and often biased) observation of single predation events. Moreover, in some cases, researchers have been able to discern different kinds of predators by examining teeth marks left on the replica models (Brodie 1993; McMillan and Irschick, in press). In short, these methods offer one more class of experimental field techniques allowing researchers to understand the causes of mortality in their study population. Given that the majority of selection studies (see Kingsolver et al. 2001 for a review) present little or no information on potential causes of mortality, one should not discount the ability of replacement methods to fill this void. As discussed later, replacement methods also offer severe limitations that should be weighed carefully against potential benefits.

#### EXAMPLES

Several studies have successfully used clay or plasticine replicas for assessing the relative risk of mortality in natural populations (Brodie 1993; Pfenning et al. 2001; Husak et al. 2006; McMillan and Irschick, in press). Replicas are typically left in the field for a set period of time (e.g., seventy-two hours), after which the numbers and types of bites are recorded. Replacement studies can be “controlled” in an experimental sense, such as by introducing nondescript items (i.e., a round piece of clay) that serve as a comparison to clay models that mimic actual prey.

Lincoln Brower and colleagues (Brower et al. 1967; Cook et al. 1967) were early pioneers in the use of this type of manipulation to characterize selection in nature. They were interested in the evolution of model-mimic complexes in Lepidoptera and in the role of bird predation in selecting for the evolution of mimicry. They performed a series of experiments in which they created artificial mimics and modified nonmimics, and then released them into the natural environment to assess their survivorship using mark-recapture methods. They also scored recaptured moths to determine if they had survived attacks by birds. In one series of experiments, the fore and hind wings of palatable mimics were painted with conspicuously colored stripes on the outer margin that made them resemble unpalatable models; controls were painted in the same area, but with colors that made them conspicuous without mimicking an unpalatable species. Their goal was to compare survival between the experimental and control moths to see if mimetic moths had a higher probability of recapture and hence survival. The overarching message of these experiments was that the mimics sometimes have a transient advantage, but the data also revealed how difficult it is to perform such manipulations in nature. Predators quickly learned that mimics were edible, so the advantage only lasted for a short while. It also proved difficult to generate sufficient sample sizes without increasing prey density to the point that might cause changes in predator behavior.

Edmund D. Brodie III (Brodie 1993), as well as David Pfenning and his colleagues (Pfenning et al. 2001), have used replicas of snakes to test ideas regarding the evolution

of mimicry. Coral snakes are highly venomous snakes that display bright alternating colored bands as a warning signal to predators. Although there exist a variety of different coral snake species, each with unique color patterns, certain species are notable for coexisting alongside nonvenomous “mimics” (typically colubrid snakes) that have evolved similar banding and color patterns (Brodie 1993). Brodie (1993) used clay replicas to test the hypothesis that predators should avoid not only venomous coral snakes (as judged by banding and color patterns on the clay replica) but also replicas of their mimics, which co-occur geographically with the coral snakes and have color patterns that are similar to those of the coral snakes. As predicted, predators avoided not only replicas showing the actual coral snake pattern but also replicas showing the mimic pattern. Predators regularly attacked a “control” replica that mimicked a harmless and similarly sized snake. The inference that predators avoided the coral snake mimics is thus derived from their lower susceptibility to attack relative to the nonmimetic “control” replicas.

The coral snake–mimic story is fascinating because of its complex geographic patterns. Alongside the eastern seaboard of the United States, coral snakes occur in the southern region, but not the northern. However, potential mimics, such as the milk snake (*Lampropeltis triangulum*) and the scarlet snake (*Cemaphora*) occur both in southern and northern regions, and therefore, one might expect that the mimics would exhibit colors similar to coral snakes in the South, but not the North. Red milk snakes (*Lampropeltis triangulum*) found north of the range of the coral snake have a nonmimetic, saddle-back pattern of blotches; populations that co-occur with coral snakes are banded in a fashion that mimics coral snakes. Likewise, other species of apparently mimetic snakes, such as the scarlet snake, have ranges that broadly overlap with the coral snake. Pfenning et al. (2001) tested whether the distribution of mimetic versus nonmimetic king snakes was shaped by patterns of mimic avoidance by placing the same set of replicas along a North-South gradient along the eastern seaboard of the United States. Pfenning et al. (2001) showed that the relative “avoidance” (as judged by the number of predator bites) of the coral snake pattern, as well as the mimic pattern that has apparently evolved along side it, diminishes from South to North, which is consistent with the known distribution of coral snakes. This work supports the view that predators are adapted to local prey assemblages and that banded color patterns of southern populations of some harmless snakes that co-occur with coral snakes evolved to be mimetic of coral snakes.

The risk of injury to an individual in some species may be caused by conspecifics, such as through male-male combat for territories. Relatively few studies have simultaneously quantified the intensity of sexual and natural selection, and even fewer have examined how the relative intensities of both processes change both seasonally (i.e., breeding season vs. nonbreeding season) and across different populations (Svensson et al. 2006). For animals with distinct breeding seasons, one might predict that the relative intensities of sexual and natural selection should peak at the same time (i.e., during the breeding/growing season). From a spatial perspective, there is reason to predict trade-offs in the

relative intensity of sexual versus natural selection. In populations in which predation is high, the intensity of sexual selection, particularly male competition, may be dampened because of the inherent risks assumed by males when competing (e.g., conspicuous displays).

Recent work in Duncan Irschick's laboratory tested these possibilities using replica models of green anole lizards (*Anolis carolinensis*). Within polygynous lizards, such as green anoles, male competition is the predominant factor that determines reproductive opportunities (Tokarz 1995). Green anoles will often bite one another during agonistic fights, which take place primarily during the spring breeding season (Jenssen et al. 2001; Lailvaux et al. 2004). McMillan and Irschick (in press) placed clay models mimicking adult male green anoles in natural habitats, and then observed bites from both predators (e.g., birds) and competing male green anoles. This experiment was replicated across different seasons (spring, fall, and winter) and in two divergent populations. One population was an urban site in which male competition was predicted to be unusually intense, and predation was predicted to be relatively low (Bloch and Irschick 2006), whereas the other population was a more natural field site in which natural predators were more common, although the intensity of sexual selection was poorly understood. As predicted, the intensity of male competition (the number of bites from green anole males) was highest during the spring, intermediate in the fall, and lowest during the winter, and predator bites followed a similar pattern. These results support the view that sexual and natural selection "peak" during the warmer breeding season, and then together decline during the nonbreeding season. On the other hand, although there was some evidence that the intensity of male competition was extremely high in the urban population with few predators, the intensity of male competition was also very high in the more natural field site with more predators.

Finally, Husak et al. (2006) used clay models of collared lizards (*Crotaphytus collaris*) in three different populations that differ in their average degree of coloration. Male collared lizards exhibit bright colors that act as sexual signals, and females are far less colorful. The role of color in these collared lizards is not well understood, but in many male lizards, there is strong selection for bright colors that may signal male quality to females (Lailvaux and Irschick 2006). Therefore, any predation cost on bright colors implies a cost associated with a sexually selected trait. Husak et al. (2006) tested the hypothesis that more colorful individuals, particularly those that contrast with their environment, suffer an increased cost of predation by building colorful clay models and noting the number of predator marks within each of the three populations. They found that at each of the three populations, more colorful individuals that were in contrast to their environment incurred higher rates of predator bites compared to less colorful models of female lizards. This work characterizes one side of the potential interplay between sexual and natural selection, and it implies a definite cost from the perspective of natural selection on sexually selected traits. If male brightness evolved because it enhanced mating success, then this study shows that it did so in the face of increased susceptibility to predation.

### CONSIDERATIONS

The clay models offer one primary advantage over the use of live animals: because the replicas do not move, and because they are designed to show marks, one can obtain reasonable estimates of the degree of predation or male competition that might otherwise be difficult, or impossible, to acquire. The “modified” animals employed by Brower and colleagues offer the ability to manipulate the phenotypes of natural populations yet maintain some of the mobility and natural behavior of live animals, thus enhancing the ability to determine how selection operates on populations via predation.

The clay model method, in particular, presents shortcomings that need to be considered by researchers. First, the index of predation intensity gained is unlikely to represent a complete profile of all potential predators. For example, some predators focus on movement or smell, and therefore replicas may not be effective for examining how such predators capture prey. Second, the interpretation of the bites themselves can be challenging. While the approximate size and shape of the bites provide rough information on the kind of predator involved (e.g., bird vs. rodent), they provide limited information about the species of predator or the attributes of individual predators, such as their age or size, and hence limit one’s ability to make inferences about their likely experience. Third, one cannot discount the possibility that the same predator or conspecific might bite a model multiple times. Therefore, analysis of bites should be conservative and perhaps consider just the proportion of replicas that are attacked rather than the number of attacks per replica. The motive of the bites is not known; one must consider the possibility that some bites may arise more out of curiosity than an actual intent to kill and eat.

### LIVE ANIMAL INTRODUCTIONS

#### BACKGROUND

Live animal introductions (i.e., transplant experiments) involve the transfer, either intentional or unintentional, of live organisms from their source population to another geographic location. Here we distinguish between “human-planned” introductions, usually done in the context of a field experiment, and “unplanned natural” experiments, which amount to the introduction (either planned or unplanned, but usually undertaken haphazardly) of species into novel environments. Intentional introductions of animals often occur for reasons such as biological control, and unintentional introductions often represent “invasive” species that have moved into new habitats by various means. We do not review plant studies here even though experimental transplant experiments have been widely used by plant biologists. However, plant studies have primarily been used as a way of evaluating the extent to which natural populations of plants differ genetically from one another and are adapted to their local environment, rather than to study how plants evolve in response to “novel” environments.

## EXAMPLES

*“Planned” Experiments* There are three successful examples of investigators transplanting populations to habitats from which the species was initially absent, then evaluating the evolution of the introduced population by using the source population as a control and evaluating the differences between the source and derived populations.

Losos et al. (1997) examined the evolutionary outcome from a planned introduction of a propagule of the naturally invasive anole *A. sagrei* onto replicate small Bahamian islands. During 1977 and 1981, Thomas Schoener and his colleagues introduced propagules of five or ten adult *A. sagrei* lizards onto fourteen islands from a larger “mainland” island that represented the “source” of the invasion. Losos et al. (1997) evaluated evolution by comparing the morphological characteristics of samples of the “mainland” (control) source versus the introduced island populations. During the intervening 10–14 years, the introduced *A. sagrei* population proliferated and also apparently evolved a significantly different phenotype relative to the mainland control. Losos et al. (1997) detected a slight but statistically significant decrease in hind limb length in the introduced population relative to the mainland source. This phenotypic change was potentially important because of the influence of hind limb length on both sprint speed (Irschick and Losos 1999) and average perch diameter usage. Losos et al. (1997) interpreted the smaller hind limbs as evidence of adaption to the use of relatively narrow surfaces, which were prevalent on the small island. Later work (Losos et al. 2000) suggested that this change in limb proportions may have arisen via plasticity because young *A. sagrei* that were raised on narrow twigs tended also to have relatively shorter limbs as adults. Regardless, this work represents a case of either rapid evolution in morphology or potentially a plastic adaptive response.

Reznick and colleagues (Reznick and Endler 1982; Reznick and Bryga 1987; Reznick et al. 1990) have used transplant studies with Trinidad guppies to evaluate the role of predation in guppy life-history evolution. Guppies are found in natural communities where they occur with different abundances and species of predators. Reznick and colleagues contrasted guppies from low predation environments and one type of high-predation community. Low-predation environments are either headwater streams or portions of streams above barrier waterfalls that exclude predators but not guppies. High-predation environments are generally found in the lower regions of drainages, below any such barriers. This contrast between low- and high-predation environments is replicated across drainages. Reznick and colleagues, and John Endler before them, transplanted guppies from a high-predation environment over barrier waterfalls that excluded both guppies and predators. Reznick and colleagues also attained the reciprocal treatment by transplanting predators over a waterfall that excluded predators, but not guppies. Their primary interest was in testing basic tenets of life-history theory—namely, whether the risk of mortality from predation (or any other extrinsic source of mortality) affected the evolution of reproductive effort and age at maturity. Specifically, increased

risk of mortality is predicted to favor those individuals that mature at an earlier age and have higher levels of reproductive effort. Thus, over human life spans, these predictions were upheld in the transplanted populations, providing strong support for key aspects of life-history theory (Reznick et al. 1997). This work represents one of the most compelling examples for how rapid evolution by natural selection can occur (Hendry and Kinnison 1999).

A recent study reveals strong evidence for rapid evolution resulting from transplanted animals, and it also shows that the evolution of brand-new morphological traits can appear in human time scales (Herrel et al. 2008). In 1971, a team of biologists led by Eviatar Nevo performed a reciprocal transplant between two islands (Nevo et al. 1972). Prior to the transplant, each of these adjacent islands (Pod Mrcaru and Pod Kopiste) had their own population of lizards (*Podarcis melliselensis* and *P. sicula*, respectively). These two species overlap broadly across various parts of the Adriatic coast and are competitors, with *P. sicula* typically displacing *P. melliselensis* out of available habitats. Nevo et al. performed a reciprocal transplant; they placed five male-female pairs on each island, with the source being the other island. In 2004, these islands were resampled, and genetic analyses showed that only the introduction of the invasive *P. sicula* onto Pod Mrcaru (formerly *P. melliselensis* habitat) was successful, and the original ten descendants had resulted in more than five thousand individuals (A. Herrel, unpublished data). In comparisons between the source island of Pod Kopiste and the introduced site of Pod Mrcaru, individuals on the latter introduced site had relatively longer and wider jaws, harder bites, and enlarged gut structures (caecal valves) that were not present in the source population (Herrel et al. 2008). Dietary analysis showed that the introduced *P. sicula* consumed more plant matter than lizards on their source island, and the enlarged jaws and enhanced bites were likely adaptive for allowing lizards to more effectively bite and chew tough fibrous plant matter. Moreover, the presence of novel caecal valves in the introduced *P. sicula* is consistent with a plant-based diet, as such structures are typically found in herbivorous lizard families (Herrel et al. 2008). The fact that the caecal valves were found in extremely young juvenile *P. sicula* from Pod Mrcaru is evidence both for genetic adaptation and against the possibility of a plastic effect from lizards eating plants from birth. While the other transplant studies noted earlier (brown anoles and Trinidad guppies) have each documented rapid evolution, Herrel et al.'s (2008) study is unique in revealing that populations can evolve novel and complex physical traits within human life spans.

A final, somewhat divergent example merits mention. Malhotra and Thorpe (1991) performed a manipulative experiment with different geographic races of the anole lizard *Anolis oculatus* on the island of Dominica. They transplanted samples of different races (e.g., highland, lowland) into alternative habitats and monitored survival in large enclosures. They found that the degree to which the introduced race survived was a function of how different that habitat was from its original habitat. In other words, lizards placed in a very different habitat from the one they were from (i.e., highland lizards placed into

a lowland environment enclosure) were less likely to survive compared to lizards placed in environment enclosures that were similar to their own. This study departs from the research described earlier in not clearly demonstrating evolution, although the study is valuable in demonstrating that natural selection seems to favor the fit between lizards and the habitat in which they originally evolved.

*“Unplanned Natural” Experiments* There are numerous examples of species moving into novel habitats (either human induced or not), but relatively few well-understood examples of how such introductions have resulted in evolutionary change.

One of the most widespread forms of purposeful human introductions of animals consists of introduced fish stocks. Because there is good information on the dates of the introductions of fish stocks, one can examine both the extent of overall phenotypic and genetic differentiation, and also the potential for formation of new species, a process that could likely become more commonplace in the context of global pattern of climate change. Hendry et al. (2000) examined several populations of sockeye salmon (*Oncorhynchus nerka*) that were relatively recently derived (introduction dates: 1937–1945 for one population, ca. 1957 for another) from an “ancestral” wild stock, and showed strong evidence for evolution of reproductive isolation in one more “derived” stock. The introduced fish have apparently diverged into distinct populations that either migrate upstream to breed or breed on beaches in the lake that they were introduced to. These different breeding sites incorporate a difference in the balance between sexual selection for males with laterally compressed bodies versus natural selection for males with shallower bodies that can survive upstream migration; the population that breeds in the lake has males with far deeper bodies than the population that migrates upstream to breed. This change in body shape, in association with female preferences, is now associated with a reduced probability of interbreeding between the two ecotypes. This result suggests that human manipulation of populations may be causing the evolution of reproductive isolation. Such isolation is in turn a key step in the formation of a new species.

The soapberry bug represents one of the most well-cited examples of unintentional introductions that have resulted in rapid evolution. Soapberry bugs (*Jadera haematoloma*) suck juice from small fruits (soapberries) contained within inflated seed pods. In order for the bug to successfully feed, its beak needs to be long enough to access the seed inside of the seed pod. For example, the fruits of the soapberry plant are like an inflated paper lantern with a seed placed near the center. Natural populations of bugs that feed on different species of plants have beak lengths that are in proportion to how inflated the seed pod is. Those that feed on plants with relatively small seed containers have relatively short beaks in comparison to those that feed on plants with highly inflated seed containers. Scott Carroll and colleagues (Carroll and Boyd 1992; Carroll et al. 1998; Carroll et al. 2003) have studied the ecology and evolution of a dramatic shift from soapberry bugs using an ancestral large fruit to a new host. The new host in Florida is the introduced golden rain tree, which has relatively flat seed pods in comparison to those

found on the native soapberry vine. The range of dates of the introduction of golden rain trees is known. The evolutionary response of the bugs was evaluated in two ways; with the measurement of periodic samples of bugs that were preserved in museum collections and through the comparison of live bugs collected from both hosts. The museum collections enabled Carroll and his colleagues to evaluate the time course of change in beak length and other aspects of morphology. The comparisons of live bugs from the alternative hosts has enabled them to show that not only has beak length changed, but the genetic architecture of this phenotypic difference has also evolved, and in a complex fashion. Furthermore, these different populations of soapberry bugs have each evolved to perform best (feed and grow) on their host plants. The native population has significantly higher fitness on the native host, while the "transplanted" population has significantly higher fitness on the introduced host. This example shows how adaptation to new ecological conditions can be both rapid and complex in terms of overall differences in the phenotype and the genotype.

Some species of copepods (small invertebrates, *Eurytemora affinis*) have invaded freshwater locations from natural saltwater habitats in the Gulf Coast and the Atlantic Ocean (Lee 1999). This repeated invasion of freshwater environments from saltwater represents a dramatic physiological change in the capacity of these invertebrates to adapt to the low salinity of fresh water. Lee (1999) studied the invasive pathways of these copepods in several ways. First, she reconstructed the phylogenetic pattern of invasion based on mitochondrial DNA sequences. Her tree included samples of copepods collected from throughout their range, as well as samples from several freshwater sites containing invasive populations of copepods. She found that the invasive populations were always genetically more similar to the native populations found within close proximity of the invaded locality than to those found elsewhere. From this pattern, she inferred that each freshwater invasion was derived from that local population. This phylogenetic tree thus clearly confirmed multiple invasions into freshwater habitats from saltwater, indicating the facility with which these animals are able to adapt to fresh water. Laboratory experiments focused on whether all of the invasive populations were equally capable of tolerating fresh water (i.e., no salinity). For the most part, invasive populations of copepods were superior in tolerating freshwater conditions compared to marine-derived populations, suggesting that local adaptation has occurred in a relatively brief period of time. This view of genetic divergence driven by natural selection was supported by evidence that, for the few cases evaluated, Lee detected reproductive isolation between the invaders and presumed ancestors. There was, however, some variation in the ability of invasive populations to tolerate freshwater environments, suggesting significant genetic variation for the capacity to invade new areas (Lee and Bell 1999).

Two final noteworthy examples are rapid evolution in wing morphology in *Drosophila* and the evolution of geographic races in house sparrows. In the old world, *Drosophila subobscura* exhibits a clinal increase in wing size with latitude. These flies were introduced into the New World (South America) around 1980, but no parallel cline

was observed in these introduced populations one decade after their introduction; yet between 1990 and 2000, a rapid cline came into existence that is similar to that observed in the Old World (Huey et al. 2000). This study suggests that evolution is both predictable and rapid, at least in terms of geographic clines.

A classic example of evolution resulting from rapid range expansion is the European house sparrow (*Passer domesticus*). This species did not colonize North America until 1852 when an initial breeding population was found in New York. That population of house sparrows rapidly expanded their geographic range, reaching Vancouver by 1900, Mexico around 1933, and Central America around 1974. This species now occurs across most of the continent, and during this rapid range expansion, this species also rapidly evolved into geographic races that differ in color as well as wing and bill morphology (Johnston and Selander 1962). These rapid physical changes, which occurred over about fifty years (Johnston and Selander 1962) are convergent with native species and seem to follow predictive geographic rules (e.g., Bergmann's rule). Taken together, both bodies of work show that widespread geographic variation can arise quickly, suggesting local adaptation at multiple different scales.

#### CONSIDERATIONS

“Human-planned” and “unplanned natural” introductions each present their own set of rewards and challenges for biologists to consider. The primary advantage of human-planned introductions is that they provide the opportunity to observe ecological interactions and their possible evolutionary responses under the watchful eye of the human experimenter, as opposed to operating on nature's own whim and time scale. Such manipulations offer the researcher at least the potential for controlling the nature of the introduced population (e.g., body size, sex ratio), although in many cases, decisions on initial conditions may be made more on practical grounds than on experimental ones. Most important, the researcher has the opportunity to quantify the intensity of natural selection and direction and tempo of evolutionary change.

The primary disadvantage to planned introductions is also an advantage of most unplanned natural introductions: time. Although rapid evolution is well documented over quite short time periods (less than fifteen years, Hendry and Kinnison 1999), the likelihood that significant evolution will occur within a practical time interval may be small. Such introductions thus benefit from prior knowledge of the likely intensity of selection and the biology of the study organism, particularly its population dynamics and generation time. Other potential disadvantages must also be considered. Some organisms may not transplant successfully because of aspects of their behavior or reproductive biology. For example, survival and successful reproduction may be too closely tied to some prior knowledge of the territory. Another concern is the nature of the actual founding populations. Care must be taken to ensure that the introduced animals are representative of the population that they are derived from and that will be used as a control for evaluating evolution after the introduction.

In all human-planned introductions and some natural unplanned introductions, researchers are afforded an opportunity to study local adaptation when one knows both the source of the introduced population and when the introduction was made. In cases like the salmon work by Hendry and colleagues (2000), researchers have been able to study the evolution of organisms over a time scale of decades that would not be accessible to an individual investigator. This means that researchers can study evolution in organisms with relatively long generation times, at least relative to a guppy or *Anolis* lizard, and hence expand our knowledge beyond what one could argue are special cases. However, key details on any introduction are often difficult to nail down, such as when it occurred; the nature of the introduced population; whether any subsequent, possibly inadvertent, introductions were made; and what the history of population growth of the introduced population was. Moreover, there is substantial difficulty in establishing a control for the evaluation of evolution in the introduced population. In the salmon example, we can evaluate the fish from the hatchery that they were derived from to provide a control, but we will have at best incomplete information on what that population was like at the time that the introduction was made or the extent to which that population may have changed in the interim.

The nature of invasive species is also inherently fascinating for evolutionary biologists because of their tantalizing similarity to natural patterns of colonization, which have characterized natural ecosystems for millions of years (Strauss et al. 2006). A significant amount of research has centered on traits of invasive species and whether good invaders exhibit unique physiological and ecological traits, for example. This also suggests caution against over interpretation, as evolutionary changes in invasive species may not be typical of most species.

A final challenge is to define the actual cause-and-effect relationships that underlie any observed evolution. Any manipulation of the environment potentially incurs a combination of direct and indirect effects. For example, guppies that are transplanted from a high-predation site into a previously guppy-free low-predation site above a barrier waterfall will experience a reduction in mortality rate, which is the presumed source of selection for life-history evolution. However, they will also predictably experience an increase in population density and a reduction in per capita resource availability (Reznick et al. 2001). Defining the relative importance of the direct effect of predators, versus the potential indirect effects, is an added hurdle that has yet to be cleared.

#### **WHAT CAN WE LEARN FROM FIELD EXPERIMENTS THAT WE CANNOT LEARN FROM LABORATORY STUDIES?**

Prior authors (e.g., Hurlbert 1984) have emphasized the importance of rigorous experimental design during field experiments (e.g., controlled conditions, replication), which is often difficult to attain. This debate has also manifested itself in prior arguments about the efficacy of historical versus contemporary approaches (Leroi et al. 1994; Reeve

and Sherman 1993; but see Larson and Losos 1996 for an opposing view). These divergent views have also revealed themselves in the debate over studies of “experimental evolution,” which are typically conducted in controlled laboratory experiments with organisms that have short generation times and can be easily bred (e.g., Bennett et al. 1990; Travisano et al. 1995). Following others (e.g., Reznick and Ghalambor 2005; Carroll et al. 2007), we take the perspective that introductions—whether planned, unplanned, intentional, or unintentional—present a source of material for understanding rapid evolution. We also feel that the field studies outlined in this review are complementary to controlled laboratory experiments with microorganisms. As the breadth of the chapters in this volume shows, such experimental laboratory approaches, particularly in the context of evolution, have blossomed tremendously over the past ten years or so. In direct contrast to this rapid growth in laboratory experimental studies of evolution, we have not observed a similar growth in the number of carefully designed field introduction on animal species. In this context, we list several areas that field experimental studies of evolution have the unique capacity to address.

#### MECHANISMS OF POPULATION ESTABLISHMENT

While research has established some salient features of how small groups of individuals become established in novel areas, we know little about the manner in which these populations grow and adapt to new surroundings. Introduction experiments offer a window into processes that impact the earliest stages of population establishment, growth, and genetic differentiation, and they may also provide information about speciation (Otte and Endler 1989; Templeton 1989). Most natural or unnatural field experiments involve a clear “before and after” approach in which the populations are compared as point samples between time periods (Losos et al. 1997; Herrel et al. 2008), and therefore there is little information on early stages of population establishment. Furthermore, some authors (Garland and Kelly 2006) have noted the importance of plastic responses to the environment in studies of experimental evolution. Plastic effects are typically controlled for in laboratory studies of experimental evolution, but these effects are likely to be important in natural settings for enabling organisms to survive in difficult circumstances. For example, the rapid evolution of novel gut structures (caecal valves) in *Podarcis* lizards (Herrel et al. 2008) begs the question about when these structures first arose in the population, how many individuals first evolved them, and what the genetic architecture underlying this complex trait was composed of (this last point is important because Herrel et al. [2008] did not clearly demonstrate that caecal valves possessed a genetic basis). Transplants with repeated sampling (i.e., yearly) over long time periods offer the promise for understanding these early stages of growth, plastic responses, and genetic differentiation, and the delayed hope for an evolutionary response that is discernible to human eyes.

Selection during the early course of population establishment is likely to be dynamic, and there is potential for interplay between habitat choice and morphological evolution.

For instance, in manipulative studies with a predator (the curly-tailed lizard, *Leiocephalus carinatus*) and its prey (the brown anole, *A. sagrei*), selection initially favored longer limb length in *Anolis* when they are first exposed to a predator, but selection later favored shorter limbs as prey populations shift to a more arboreal lifestyle, possibly to elude the predator (Losos et al. 2006). Intensive sampling of transplanted populations can capture these subtle interrelationships among habitat use, morphology, and species interactions. Ideally, therefore, researchers should gather ecological data on transplanted populations over a period of time to determine if there is a dynamic interplay for selection on morphology, habitat use, and the interaction between the two.

#### RAPID EVOLUTION

In an era of increasing global changes in habitat and climate, the topic of “rapid” evolution has become prominent in the evolutionary community (Hendry and Kinnison 1999; Carroll et al. 2007). Past reviews have shown that selection in nature can often be surprisingly strong (Endler 1986; Hoekstra et al. 2001; Kingsolver et al. 2001; Hereford et al. 2004), leading to many cases of “rapid” evolution observed in the modern era (Hendry and Kinnison 1999). As a caveat, direct observations of evolutionary change yield faster estimates than those seen in the fossil record or inferred from historical introductions. The reason is that longer-term estimates average intervals when the rates vary, when direction may be reversed, and when there is no evolution. Furthermore, long-term field studies show that the pace of evolution can be remarkably high in one direction in one year and then show the opposite trend the other year (Grant 1999). In other words, researchers should interpret short-term evolutionary studies with caution.

Nonetheless, as noted in a recent special issue of *Functional Ecology* devoted to “Evolution on Ecological Time-Scales,” researchers are increasingly turning from the view that evolution is a historical phenomenon that cannot be studied in human life spans (Carroll et al. 2007). Recent work also shows that species may be able to evolve novel structures in human life spans, although more work is needed to verify this exciting possibility (Herrel et al. 2008). Moreover, in an era of ever-increasing human contact, the rapid movement of animal and plant species ensures that invasive species will continue to challenge efforts to preserve “natural” habitats and suites of species. Added to this phenomenon of the movement of species is the potential for both introduced species, and the species they affect, to evolve, in essence providing a moving target for researchers interested in biological control (Carroll et al. 2007).

Quantifying the “rate” of evolution is challenging given the diversity of different traits and taxa that researchers have examined. Previous authors have primarily used two standardized metrics: the Darwin and the Haldane. Hendry and Kinnison (1999) presented data for such values across widely disparate taxa (fish, insects, lizards) from both the fossil record and present-day field introductions and microevolution. Based on their analysis, as well as simple calculations completed in Herrel et al. (2008), all three of the planned

field experiments discussed here provide some of the most rapid estimates of evolution discussed to date (Hendry and Kinnison 1999; Herrel et al. 2008), suggesting that the “payoff” for such difficult studies is substantial. Moreover, some of the other commonly discussed examples of rapid evolution come from studies of introduced species (Hendry and Kinnison 1999), such as in salmon and birds. The reasons for such rapid evolution in introduced species seems obvious: in order for species to effectively live in a new environment, rapid change is often necessary, such as in salinity preferences in copepods (Lee 1999), yet there is also the possibility that the capacity for such rapid evolution is a hallmark of highly invasive species and is not typical for species that have more specific habitat preferences (Cox 2004).

#### NATURAL AND UNNATURAL HABITAT ALTERATIONS

Habitat alteration, in the form of either natural catastrophic events or human alteration, has long been recognized as having a significant impact on ecological dynamics and, more recently, evolutionary dynamics (Hendry et al. 2006). Catastrophic events, such as major storms, volcanic explosions, and earthquakes, among others, have played an important role in the “unraveling” of the history of life (Gould 1989); in an era of global warming, such events promise to become increasingly important for modern ecological communities. For example, one cited consequence of global warming is a greater frequency and strength of hurricanes, such as those that commonly occur on the Gulf Coast of North America. Recent work has shown that major hurricanes in the Bahamas have the potential to dramatically reshape lizard populations, particularly if the hurricane strikes during periods when populations are vulnerable, such as during the reproductive season (Schoener et al. 2004). How these disturbances affect the evolution of these populations is not yet known however and is a topic of current investigation (J. Losos, personal communication). In the context of field experiments and evolution, catastrophes have the potential to provide a nearly unlimited number of natural experiments, and they certainly have the potential to speed up rates of evolution. We believe that this avenue has barely been explored, but the possibilities are unlimited. Especially valuable would be studies that can show how catastrophic events alter the course by which selection operates, like a powerful wind that alters the course of a ship. This kind of data would likely only emerge from researchers that already have good long-term field data and data on which a catastrophe fortuitously (or not so fortuitously, for the study organisms) strikes.

While not spectacular in the same vein as a hurricane or earthquake, dramatic human disturbance can be catastrophic to local animal and plant populations, and recent work by Hendry et al. (2006) hints that such disturbance may actually be dampening the rate of evolutionary divergence. They examined two populations of Darwin’s finches, one of which occurs in relatively natural settings apart from human disturbance, whereas the other has experienced significant human disturbance over the past thirty years. Hendry et al. (2006) found that human activity may be “dampening” morphological variation in

the human-disturbed population by diminishing the presence of discrete bird morphs, whereas the more natural population experienced a higher degree of morphological variation. This finding highlights an unexpected consequence of catastrophic changes to habitat structure—namely, a slowing down of evolution.

## CONCLUSION

The increasing trend of global warming and climate change on earth means that future transplant experiments in nature offer the potential for detecting rapid evolution over human life spans (Carroll et al. 2007), and we would like to see this class of data grow both in number and taxonomic breadth (two of the three transplant studies mentioned here were on lizards, one on fish). In this vein, we point toward several areas of research that would expand our knowledge base on how small populations become established, grow, and evolve, in novel environments.

First, more research that examines processes of population establishment, growth, and genetic change would give a window into whether plastic responses (Garland and Kelly 2006) enable organisms to survive or, alternatively, whether evolution begins to occur almost immediately.

Second, research that places different genetic lines into different environments to test alternative hypotheses on how different genetic backgrounds respond to selection would be welcome. Because different genotypes might respond differently to the same selective pressure, intentional field introductions of a mix of genotypes, along with subsequent sampling, would establish not just selection on phenotypes but also selection on genotypes, and perhaps plastic responses as well (Goodnight 1988). This avenue offers the best way for researchers to test classic population genetic models of population divergence and speciation in a natural setting, and the rapidly expanding genetic tool kit available to researchers should make such manipulations possible in a wide array of organisms.

Third, evolutionary ecologists should also consider joining forces with natural resource managers who regularly monitor natural populations and their patterns of life and death. Given recent work showing very strong selection on horn morphology in bighorn rams (Coltman et al. 2002), there is ample opportunity for observing humans as a strong selective force on animal populations, with the potential for subsequent evolution.

Finally, we remind the reader of the importance of carefully considering the ethical implications of natural introductions. Because of rapid climate change on earth, introductions of certain species, even into seemingly remote locations, might be disastrous, especially for highly invasive species that are introduced near the edge of their ranges. We note that in all three planned transplant experiments (experiments with *Anolis* lizards, Trinidad guppies, and Italian wall lizards), each of these species was unlikely to disturb the larger ecological community following the transplant. Ensuring that field experiments are conducted with minimal long-term consequences for other plant or animal species should be of paramount importance.

## SUMMARY

Field experimental evolution studies have served as an important complement to more common descriptive evolutionary studies. Our goal is to provide a practical guide for researchers interested in experimental evolution and field introductions. We distinguish between “replacement” experimental methods, which employ fake (replica) organisms that are assessed for environmental effects (e.g., predator bites), and the introduction of live organisms into novel habitats. While relatively few studies have purposefully designed experiments for examining evolutionary change, there are many examples of “unplanned natural” experiments, such as human introductions for pest control. Replacement experiments provide a useful method for studying the effects of predation, and they have been used to test ideas about mimicry, the contributions of natural and sexual selection, and the costs of extravagant colors. Planned experiments show that evolution in introduced populations can be extremely rapid, suggesting that the initial investment in time toward such experiments is worthwhile. Recent studies also show that even new phenotypic traits can evolve over human life spans. Finally, different populations of invasive species are not equally successful for evolving effective specializations for new habitats.

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