



The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution

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Abstract

Under what conditions might organisms be capable of rapid adaptive evolution? We reviewed published studies documenting contemporary adaptations in natural populations and looked for general patterns in the population ecological causes. We found that studies of contemporary adaptation fall into two general settings: (1) colonization of new environments that established newly adapted populations, and (2) local adaptations within the context of a heterogeneous environments and metapopulation structure. Local ecological processes associated with colonizations and introductions included exposure to: (1) a novel host or food resource; (2) a new biophysical environment; (3) a new predator community; and (4) a new coexisting competitor. The new environments that were colonized often had depauperate communities, sometimes because of anthropogenic disturbance. Local adaptation in heterogeneous environments was also often associated with recent anthropogenic changes, such as insecticide and herbicide resistance, or industrial melanism. A common feature of many examples is the combination of directional selection with at least a short-term opportunity for population growth. We suggest that such opportunities for population growth may be a key factor that promotes rapid evolution, since directional selection might otherwise be expected to cause population decline and create the potential for local extinction, which is an ever-present alternative to local adaptation. We also address the large discrepancy between the rate of evolution observed in contemporary studies and the apparent rate of evolution seen in the fossil record.

Introduction

How fast can organisms evolve and what conditions are conducive to adaptive evolution? A traditional Darwinian perspective is that evolution by natural selection is a slow process that can, with time, result in adaptation and substantial change. Darwin (1859) based this perception on the abundant evidence that evolution had happened and that organisms have the capacity to evolve under artificial selection, yet the process of evolution by natural selection had not been directly observed. Darwin attributed the difference between the capacity to evolve and the slower apparent rate of evolution to the weaker forces of natural selection compared to artificial selection. His expectations for the rate of evolution were derived primarily

from the fossil record, which sustained the view that evolution could be very slow, yet result in substantial change. Most of the early observations of evolution by natural selection (e.g., industrial melanism, insecticide resistance, heavy metal tolerance) were attributable to anthropogenic influences, which were believed to exert stronger than natural coefficients of selection. A common perspective was thus that such observations prove that natural selection can work, but that they do not represent how it usually works. The fossil record has thus remained a primary source of expectations for the sustained rate of evolution. For example, Haldane (1956) estimated the coefficient of selection associated with the replacement of the peppered morph by the melanic morph of *Biston betularia*, so he was well aware that evolution by natural selection could be

rapid. However, when he proposed the darwin as a unit for evaluating the rate of evolution, he applied it only to data from the fossil record. After doing so, he emphasized the "...remarkably small order of magnitude of the selective 'forces' which are at work if natural selection is responsible for evolution and the extreme difficulty of demonstrating them in action" (Haldane, 1949).

Endler (1986) argued, based upon a review of the literature, that the coefficients of selection associated with natural processes could be quite high, which also creates the expectation that evolution in nature could be fast enough to be readily observable. His expectation was correct, as measured in the growing number of reports documenting rapid evolution in natural populations. Recent reviews suggest that natural populations are capable of sustained rates of evolution many orders of magnitude higher than those observed in the fossil record (Reznick et al., 1997; Thompson, 1998; Hendry & Kinnison, 1999). These results suggest that sustained evolutionary change and its underlying processes occur fast enough to make them amenable to empirical investigation. For example, high rates of evolution make it more feasible to evaluate the sustained rate of change (Lynch & Lande, 1993; Burger & Lynch, 1995) or the association between natural selection and speciation (Schluter, 1998), and to hence evaluate the possible relationship between micro- and macroevolution. Perhaps more importantly, empirical studies of adaptive evolution provide an opportunity to observe the relevant ecological conditions that influence the course of natural selection and rate of evolutionary change, an aspect of the process that is not so readily evaluated when considering the fossil record.

Our goal here is to review empirical studies that report on contemporary adaptive evolution in natural populations and to identify whether certain ecological conditions promote rapid evolution. In so doing, we ask: 'what is the population biology context of rapid adaptation?', and 'what ecological processes result in selection pressures sufficient to cause rapid adaptation?'

Criteria for evaluating studies of contemporary adaptation

There are many ways of defining 'rapid' adaptive evolution. We have chosen to restrict our review to those studies that evaluate sustained episodes of directional

selection for which a likely cause is known and for which the response to selection is likely to be an adaptation and hence to have a genetic basis. We have been liberal in the application of the criteria for inclusion to maximize the number of cases available for evaluation. We have not restricted ourselves to cases for which it is possible to formally estimate the rate of evolution, since this was not our goal and because this allows us to increase our sample size. While we do not formally evaluate the rate of evolution, Hendry and Kinnison (1999) demonstrated that, if a response to sustained directional selection is observable during the lifetime of an investigator, then the rate of evolution is orders of magnitude faster than what is considered rapid evolution in the fossil record. We also recognize that there is evidence for strong selection and rapid evolution that does not involve sustained episodes of directional selection, such as in studies of frequency and density dependent selection in lizards (Sinervo & Lively, 1996; Sinervo, Svensson & Comendant, 2000), the distribution of sexual reproduction and clonal diversity in snails (Fox et al., 1996), or seasonal fluctuations in inversion polymorphisms in fruit flies (Powell, 1997). We will not deal with these studies either. Finally, we did not review studies of rapid molecular evolution or studies based on the fossil record.

We focused our efforts on contemporary studies of microevolution (primarily within the last 200 years) documenting changes in morphological, life history, behavioral, and physiological characters. The studies considered were almost always associated with some information about the time interval over which the change had taken place, the context of the change, and the nature of the ancestral and derived states of the trait under consideration. Thus, our assessment is focused specifically on studies demonstrating rapid 'adaptive' evolution. We made a distinction between studies documenting phenotypic change and studies that provided reasonable evidence for a genetic basis to the observed changes in the trait(s). Reasonable genetic evidence included direct and indirect estimates of trait heritability, reciprocal transplants, or common garden experiments.

Studies were evaluated based on the range of taxonomic diversity, the diversity of characters that evolved, the population biology context in which they had occurred, and the ecological processes underlying the mode of selection. Our goal was to identify patterns that might predict which taxa, characters, or conditions are associated with rapid evolution.

Overview of studies

The most obvious pattern in empirical studies documenting adaptive evolution is that most of them document the response to anthropogenic changes in the environment, most notably, heavy metal tolerance, air pollution tolerance, insecticide resistance, herbicide resistance, and industrial melanism (Table 1). These five categories of anthropogenic influences are each potentially represented by a very large number of papers dealing with many different species. For example, Kettlewell (1973) summarized industrial melanism for over 70 species in England alone, and many more from elsewhere in Europe and North America. Similarly, the evolution of heavy metal tolerance and insecticide resistance has been documented in hundreds of species around the world (e.g. Antonovics, Bradshaw & Turner, 1971; Mallet, 1989; Macnair, 1991a; Rosenheim et al., 1996). Because these topics have been reviewed in depth elsewhere, we have represented each of them with just a few representative papers and reviews and consider these sufficient to represent these forms of adaptations.

Overall, we found 47 studies documenting rapid evolution in response to both anthropogenic and natural changes in the environment (Table 1). Thirty-six of these studies document a genetic basis to the phenotypic change, while the remaining 11 only report phenotypic change in response to selection (Table 1). Studies varied in the degree to which the criteria of documenting the environmental factor responsible for evolutionary changes and the time interval over which the change took place (Table 1). Collectively, the studies span a wide range of taxa, characters, ecological conditions, and modes of selection. We first describe the results from these four perspectives.

Taxonomic distribution

Of the 47 studies reviewed, 38 describe rapid evolution in animals. This discrepancy does not reflect differences in the ability of plants and animals to respond to selection, as many of the studies documenting rapid evolution in plants are reviews that encompass many more species than those reported in Table 1. Of the 38 studies on animals, 19 dealt with at least 16 vertebrate species (eight birds, more than five fish, and two mammals), and 19 studies dealt with invertebrates (Table 1). The invertebrates were represented by numerous studies documenting adaptation to heavy metals in various annelid, mollusc, and crustacea spe-

cies (Klerks & Weis, 1987; Table 1). Of the remaining studies, we found nine studies of terrestrial insects (three diptera, two hemiptera, three lepidoptera, and one mosquito) and five studies of aquatic invertebrates (two crustaceans, and two gastropods).

Character distribution

The characters that evolved can be placed into five general categories: morphology, physiology, life history, phenology, and behavior (Table 1). Morphological traits that exhibited rapid evolution included changes in body size (e.g., Baker, 1980 in birds; Reznick, Bryga & Endler, 1990 in fish; Huey et al., 2000 in flies), feeding morphology (Carroll & Boyd, 1992 in soapberry bugs; Smith et al., 1995 in birds) and anti-predator armor (Seeley, 1986 in marine snails).

Physiological characters included salinity tolerance in copepods (Lee, 1999), heavy metal tolerance in plants and animals (Antonovics, Bradshaw & Turner, 1971; Klerks & Weis, 1987; MacNair, 1987), insecticide resistance (Rosenheim et al. 1996), and thermal tolerance (Holland et al., 1974; Hendry, Hensleigh & Reisenbichler, 1998).

In those studies where life history traits evolved, no single trait evolved in isolation, but rather a suite of traits were found to evolve in response to selection. For example, evolution of the perennial strategy from the annual strategy in the grass *Poa annua* included changes in the number and size of inflorescences and allocation of resources towards growth versus reproduction (Till-Bottraud, 1990). A similar pattern of correlated responses to selection was observed in studies of vertebrate life history evolution (Stearns, 1983a, b; Reznick, Bryga & Endler, 1990).

The timing or phenology of different traits was found to evolve in a number of plant and animal species. For example, introduced populations of *Solidago* in Europe have evolved clinal differences in flowering time that parallel environmental gradients (Weber & Schmid, 1998). Similarly, a number of insects have evolved differences in the duration of development, time at emergence, or diapause (e.g., Carroll, Dingle & Klassen, 1997; Byrne & Nichols, 1999; Groman & Pellmyr, 2000).

Finally, complex behaviors have rapidly evolved in many animals. Examples include the timing, orientation, and destination of migratory behavior in birds (Berthold et al., 1992; Able & Belthoff, 1998) or the loss of anti-predator behavior in fish that been in-

Table 1. A breakdown of studies documenting contemporary adaptation in natural populations

	Study species	Genetic basis	Population biology context	Ecological process	Evolutionary/adaptive response	Refs.
1.	Numerous bacteria spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to sediment contaminated with heavy metals	1
2.	Numerous algae spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to water contaminated with heavy metals	1
3.	Numerous fungi spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to medium contaminated with heavy metals	1
4.	<i>Pisolithus</i> fungus	Yes	Metapopulation	Colonization – new soil	Tolerance to soils contaminated with heavy metals	2
5.	Numerous plant spp. ^a	Yes	Metapopulation	Colonization – new soil	Tolerance to soils contaminated with heavy metals	3, 4
6.	Numerous plant spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to herbicides	5
7.	Numerous plant spp.	Yes	Diverse	Increase in mortality	Tolerance to air pollution	6
8.	<i>Poa</i> grass ^a	Yes	Metapopulation	Reduction in mortality	Change in life history strategies	7
9.	<i>Solidago</i> plants ^a	Yes	New isolated population	Colonization – new climate	Cline in flowering time	8
10.	Numerous insect spp. ^a	Yes	Metapopulation	Increase in mortality	Tolerance to insecticides	9
11.	<i>Acyrtosiphon</i> aphid	Yes	Metapopulation	Colonization of new host	Larval survival higher on new host	10
12.	<i>Jadera</i> bug ^a	Yes	Metapopulation	Colonization of new host	Change in beak morphology	11
13.	<i>Jadera</i> bug ^a	Yes	Metapopulation	Colonization of new host	Change in emergence time, higher performance on host	12, 13
14.	Numerous lepidoptera spp. ^a	Yes	Metapopulation	Increase in mortality	Change in frequency of cryptic morphology	14
15.	<i>Prodoxus</i> moth ^a	Yes	Metapopulation	Colonization of new host	Change in ovipositor size and shape, emergence time	15
16.	<i>Pararge</i> moth ^a	Yes	New isolated population	Colonization – new climate	Change in wing morphology	16
17.	<i>Euphydras</i> butterflies ^a	Yes	Metapopulation	Colonization of new host	Larval survival higher on new host	17
18.	<i>Culex</i> mosquitoes ^a	Yes	New isolated population	Colonization of new host	Change in diapause, mating behavior	18
19.	<i>Rhagoletis</i> fruit fly ^a	Yes	Metapopulation	Colonization of new host	Change in diapause	19

Table 1. (continued)

	Study species	Genetic basis	Population biology context	Ecological process	Evolutionary/adaptive response	Refs.
20.	<i>Drosophila</i> fruit fly ^a	Yes	New isolated population	Introduction – new climate	Cline in body size	20
21.	<i>Drosophila</i> fruit fly	Yes	New isolated population	Introduction – new climate	Cline in larvae emergence time	21
22.	Numerous annelid spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to sediment contaminated with heavy metals	1
23.	Numerous mollusc spp. ^a	Yes	Diverse	Increase in mortality	Tolerance to sediment contaminated with heavy metals	1
24.	<i>Littorina</i> snails	No	Confined population	Increase in predation	Change in shell morphology	22
25.	<i>Hydrobia</i> snails	No	New isolated population	Increased competition	Divergence in body mass between competitors	23
26.	Numerous crustacean spp. ^a	Yes	Diverse	Diverse	Tolerance to water contaminated with heavy metals	1
27.	<i>Eurytemora</i> copepod ^d	Yes	Metapopulation	Colonization of freshwater	Salinity tolerance, larval survival higher in freshwater	24
28.	<i>Diaptomous</i> copepod ^d	Yes	Confined population	Change in mortality	Change in diapause	25
29.	Numerous fish species	No	Diverse	Diverse	Tolerance for water contaminated with heavy metals	1
30.	<i>Gasterosteus</i> stickleback ^a	Yes	Confined population	Competition for food	Divergence in body shape, foraging mode	26
31.	<i>Gasterosteus</i> stickleback	Yes	Confined population	Increase in predation	Change in body armor	27
32.	<i>Poecilia</i> guppies ^a	Yes	New isolated population	Reduction in predation	Increase in male coloration	28
33.	<i>Poecilia</i> guppies ^a	Yes	New isolated population	Reduction in predation	Change in suite of life history traits	29
34.	<i>Poecilia</i> guppies ^a	Yes	New isolated population	Reduction in predation	Change in anti-predator behavior	30
35.	<i>Oncorhynchus</i> salmon	No	New isolated population	Introduction – new climate	Change in thermal sensitivity of eggs	31
36.	<i>Gambusia</i> mosquitofish	Yes	New isolated population	Reduction in mortality	Change in life history strategies	32
37.	<i>Lepomis</i> bluegill	Yes	Confined population	Increase in temperature	Change in thermal tolerance	33
38.	<i>Geospiza</i> finch ^a	Yes	Confined population	Changes in food source	Changes in bill morphology, body size	34
39.	<i>Telespiza</i> finch	No	New isolated population	Introduction – new food	Change in bill morphology	35
40.	<i>Vestiaria</i> honeycreeper	No	Metapopulation	New food source	Change in bill morphology	36

Table 1. (continued)

	Study species	Genetic basis	Population biology context	Ecological process	Evolutionary/adaptive response	Refs.
41.	<i>Passer</i> sparrows	No	New isolated population	Introduction – new climate	Cline in body size	37, 38
42.	<i>Ploceus</i> weaverbird	No	Confined population	Reduction in parasitism	Change in egg-rejection behavior	39
43.	<i>Sylvia</i> warbler ^a	Yes	New isolated population	Colonization – new climate	Change in migratory behavior	40
44.	<i>Carpodacus</i> finch	No	New isolated population	Colonization – new climate	Change in migratory behavior	41
45.	<i>Myzomela</i> honeyeaters	No	New isolated population	Increased competition	Divergence in body mass between competitors	42
46.	<i>Mus</i> mouse	No	New isolated population	Introduction – new climate	Cline in body size	43
47.	<i>Oryctolagus</i> rabbits	Yes	New isolated population	Introduction – new climate	Change in fecundity	44

References: 1. (Klerks, 1989); 2. (Egerton-Warburton et al., 1993; Egerton-Warburton & Griffin, 1995); 3. (Antonovics, Bradshaw & Turner, 1971); 4. (MacNair, 1987); 5. (Jasieniuk & Maxwell, 1994); 6. (Taylor, Pitelka & Clegg, 1991); 7. (Till-Bottraud, 1990); 8. (Weber & Schmid, 1998); 9. (Mallet, 1989); 10. (Via, Bouck & Skillman, 2000); 11. (Carroll & Boyd, 1992); 12. (Carroll, Dingle & Klassen, 1997); 13. (Carroll, Klassen & Dingle, 1998); 14. (Kettlewell, 1973); 15. (Groman & Pellmyr, 2000); 16. (Hill, Thomas & Blakeley, 1999); 17. (Singer, Thomas & Parmesan, 1993); 18. (Byrne & Nichols, 1999); 19. (Filchak, Roethele & Feder, 2000); 20. (Huey et al., 2000); 21. (James & Partridge, 1995); 22. (Seeley, 1986); 23. (Fenchel, 1975); 24. (Lee, 1999); 25. (Hairston & Walton, 1986); 26. (Schluter, 1994); 27. (Bell, Baumgartner & Olson, 1985); 28. (Endler, 1980); 29. (Reznick, Bryga & Endler, 1990); 30. (Magurran et al., 1992); 31. (Hendry, Hensleigh & Reisenbichler, 1998); 32. (Stearns, 1983a, b); 33. (Holland et al., 1974); 34. (Grant & Grant, 1995); 35. (Conant, 1988); 36. (Smith et al., 1995); 37. (Johnston & Selander, 1964, 1971); 38. (Baker, 1980); 39. (Cruz & Wiley, 1989); 40. (Berthold et al., 1992); 41. (Able & Belthoff, 1998); 42. (Diamond, 1989); 43. (Berry, 1964); 44. (Williams & Moore, 1989b; Williams & Moore, 1989a).

^aDenotes studies that provide evidence for contemporary adaptation by documenting the genetic basis to the adaptive change, the selection pressure in the environment responsible for the adaptation, and the time interval over which change has occurred. Where numerous species were reviewed, at least some species met the above criteria.

troduced to sites without predators (Magurran et al., 1992).

Population biology of rapid evolution

We found that almost all cases of contemporary adaptation were associated with ‘colonization’ events. We defined ‘colonization’ as any situation where individuals of one population become established in a previously unoccupied habitat. Events such as host shifts in insects, human introductions of plants and animals to new locations, and establishment of plants on contaminated soils all represent different types of colonizations. Of the 47 total studies, all but six were categorized as being colonizations, suggesting a strong association between rapid evolution and establishment of new populations in novel environments.

We found that colonizations occurred under two broad population biology settings. The first setting occurred when individuals colonize novel environments and establish new populations that are isolated from their ancestral populations. We categorized at least 18 studies as being representative of this type of colonization, including natural range expansions into previously uninhabited environments (e.g., Byrne & Nichols, 1999; Hill, Thomas & Blakeley, 1999), and purposeful or accidental human introductions (e.g., Baker 1980; Conant, 1988).

The second broad ecological setting occurs when a subdivided population is subjected to heterogeneous environmental conditions that create the opportunity for adaptation in local populations. We consider this second setting as representative of a metapopulation dynamic (Hanski et al., 1998) because of the mosaic nature of adaptation, although few of the studies explicitly discuss their results from this perspective. We found at least 13 studies that could be placed in a metapopulation context. We distinguished colonizations in the metapopulation context from the first category primarily on the grounds that gene flow and the opportunity for repeated colonizations are more common when the colonized environment is a modified patch within the pre-existing range of the species. The most common examples of such a process are the many cases of anthropogenic influences, such as heavy metal contamination of soils or the use of herbicides and insecticides that create new and often hostile patches of habitat within a landscape. However, the same sort of colonization occurs when insects establish populations on a new host plant within their existing range (e.g., Singer, Thomas & Parmesan, 1993; Carroll, Klassen

& Dingle, 1998; Filchak, Roethele & Feder, 2000; Groman & Pellmyr, 2000).

While we considered colonizations within a metapopulation context distinct from those that result in isolated populations, both processes may also operate within natural populations. For example, individuals that initially colonize new environments and become isolated from their ancestral populations, may later radiate and establish a metapopulation structure from which distinct populations and species arise (e.g. Losos & Schluter, 2000). However, we retain the dichotomy between these two ecological settings to describe the initial conditions under which selection acts on newly established populations.

Ecological processes and traits subject to change

Four general ecological processes were responsible for almost all cases of rapid adaptive evolution that were reviewed (Table 1). Below we consider the mode of selection associated with each of these ecological processes and some representative case studies.

Changes in host plant or food resources

Many organisms specialize on one or a small number of food resources. Switching to a new food resource can lead to sustained directional selection on traits responsible for resource acquisition and processing. We found ten studies that documented shifts in either a host plant by a phytophagous insect or a change in the predominant food source, resulting in adaptive changes in feeding morphology or associated traits (Table 1). Perhaps the most elegant demonstration of this ecological process is work by Scott Carroll and colleagues on host race formation in the seed-eating soapberry bug (*Jadera hamatoloma*). Soapberry bugs have colonized three new species of introduced plants in North America over the past century (Carroll & Boyd, 1992). Each introduced plant species has a different seed pod that requires modification of the ancestral beak length to efficiently access the seeds within the pod (Carroll & Boyd, 1992). Comparisons of ancestral soapberry bug populations on their native hosts with populations on the introduced host plants demonstrated repeated adaptive changes in the beak length that have a genetic basis (Carroll, Dingle & Klassen, 1997). Furthermore, a series of reciprocal transplants have demonstrated that each soapberry bug race is locally adapted to its host’s chemistry, suggesting that a suite of traits have evolved over a relatively short time (Carroll, Klassen & Dingle, 1998).

Changes in the bio-physical environment

Colonization is often associated with a diversity of changes in factors other than food resources that can impose directional selection. We found 11 studies that documented rapid evolution in response to a new environment (Table 1). Populations exposed to new climatic gradients can evolve clinal variation in traits such as body size (e.g., Baker, 1980; Huey et al., 2000) and phenology (e.g., James & Partridge, 1995; Quinn & Adams, 1996; Weber & Schmid, 1998.). Other important examples of this process include plant populations that have colonized and evolved tolerance to soils contaminated with heavy metals (Lefebvre & Vernet, 1991; Wu, 1991). In those cases where insects shift hosts (see above), populations are also often exposed to correlated changes in the hosts' phenology, such as the flowering season or the seasonal availability of seeds, which can in turn select for the evolution of diapause and morphology in the insect (e.g., Carrol, pers. commun.; Singer, Thomas & Parmesan, 1993, Groman & Pellmyr, 2000). The process of colonizing a new physical environment is well illustrated in the work of Lee (1999) on the copepod (*Eurytemora affinis*). *Eurytemora* is globally distributed in marine environments, but has recently invaded and become established in a number of different freshwater environments throughout different parts of its range. Transplant experiments demonstrate the substantial physiological adaptations required in the new freshwater environment, as only 1.1% of juveniles from marine environments successfully metamorphosed into adults when transplanted to freshwater (Lee, 1999). Observations on some of these colonizations indicated that adaptation to freshwater can occur within a few years.

Changes in mortality rates

Change in mortality rates, especially predator-induced mortality, can impose directional selection on traits that reduce the probability of predation or increase the probability of reproductive success in the target organism. Excluding those studies where humans are directly responsible, we found nine studies that documented rapid evolution in response to changes in mortality rates. In all but one the mortality was predator induced (Table 1). Change in mortality rates selected for adaptive changes in life history traits (Stearns, 1983a, b; Reznick, Bryga & Endler, 1990; Till-Bottraud, 1990), anti-predator behavior (Cruz & Wiley, 1989; Magurran et al., 1992), morphology (Seeley, 1986) and coloration (Endler, 1980). Long-term research on

the effects of predation on Trinidadian guppies (*Poecilia reticulata*) provides a useful framework in which to examine adaptive evolution in response to predator-induced mortality. Guppy populations from Trinidad have significant differences in color patterns, behaviors, and life histories that are strongly associated with the species of predators that they co-occur with (Reznick & Endler, 1982; Magurran et al., 1992; Endler, 1995; Reznick & Bryga, 1996). For example, female guppies from low predation environments produce fewer, larger offspring in each litter, have smaller reproductive allotments (percent body weight that consists of developing embryos), mature later, reproduce less frequently, and devote a smaller percentage of consumed resources to reproduction than their counterparts from high predation localities (Reznick, 1982; Reznick & Endler, 1982; Reznick, 1989; Magurran et al., 1992; Endler, 1995; Reznick & Bryga, 1996; Reznick & Bryga, 1996). Transplanting guppies from high to low predation environments reveals that this suite of life history traits can evolve in less than 20 generations (Reznick, Bryga & Endler, 1990; Reznick et al., 1997).

Changes in competitive interactions

Competitive interactions among species can select for character displacement and adaptive radiations (Schluter, 1996). Three studies documented the role of competition in rapid divergence among closely related species (Table 1). The most familiar example of this process is the evolution of a trophic dimorphism in the three-spine stickleback (Schluter, 1994; Schluter, 1995; Hatfield & Schluter, 1999; Vamosi, Hatfield & Schluter, 2000). Experimental and observational evidence suggests that competition between morphs is the mechanism driving the evolution of their divergence in morphology and body size. Diamond et al. (1989) described an example of the rapid origin of character divergence between the two closely related bird species, *Myzomela pammelaena* and *M. sclateri* in New Guinea. Historically, these two species of honeyeaters only lived allopatrically on different islands where they are very similar in body size (*M. sclateri* is slightly smaller in allopatry). In mid-17th century a large volcanic eruption on Long Island completely defaunated the island. Both honeyeater species have subsequently colonized and become established on the island. Comparisons of the recent sympatric populations with their allopatric counterparts revealed that *M. pammelaena* is 4–14% heavier and *M. sclateri* is 2–7% lighter when both species occur together. Be-

cause body size in honeyeaters is closely related to diet, Diamond et al. (1989) argued that the evolved differences in body size reduce competition for food and allow for coexistence, although a genetic basis for these differences has not been established.

Discussion

If we take these data at face value, then they argue that high rates of adaptive evolution, meaning rates that may be observable within the lifetime of an investigator and that are orders of magnitude faster than inferences based on the fossil record, may be a general capacity of a diversity of organisms and for a diversity of traits. If this is true, then these data also suggest that the reason evolution by natural selection is not so readily seen is not because it is too slow, but rather because it is too fast. If one is not looking in the right place at the right time and evaluating the right characters, or if circumstances do not provide the likely ancestral state to provide a frame of reference, then many of the sorts of events recorded in the above studies would be missed. The majority of these examples represent changes that are subtle and finite, in the sense that evolution is not destined to continue beyond the small effects already seen; however, they may still represent the general pattern of evolution by natural selection and can still fulfill Darwin's original expectations for the primary role of natural selection in macroevolution. Such a statement does not imply that all organisms are capable of responding to all forms of selection at all times; strong directional selection can also result in local or global extinction. It is also likely that environmental change will not necessarily elicit genetic change, as target populations may adapt through phenotypic plasticity. The key is to evaluate when rapid adaptive evolution is possible and to consider whether the small amount of data available yield any clues. Before doing so, we will first consider possible biases and limitations in our data.

Bias

Our review is dominated by colonizations, invasions, and anthropogenic modifications of the environment. This might be because these are the circumstances that attract the attention of investigators and hence that they are a biased subset of the circumstances that favor rapid adaptation. However, it may also be that these really are specific examples of more general circumstances that can promote rapid adaptive

evolution. In either case, future research should seek to evaluate how quickly populations can evolve under a broader range of natural circumstances. Given this acknowledgment, we will proceed with the spirit that these are the best available data and hence that we should consider what lessons they might offer.

Negative results

A second source of bias in our evaluation is that it does not consider negative results, or circumstances where populations have experienced directional selection but have not been successful in responding. The conditions under which there is an absence of a response or an extinction are important because they can help to define the circumstances that promote rapid adaptive evolution, but how can one define how often and under what circumstances something does not happen? Failures, such as local extinctions, could vastly outnumber the successes, yet may go unrecorded because they are less likely to attract attention. The reported cases of successful responses to directional selection are certainly a small subset of all such opportunities. Investigators may also be less inclined to report negative results or journals may be less inclined to publish them. The absence of a significant result may also be attributed to an insufficient response to be detectable within the time interval considered or the experimental approach that was employed.

In spite of these difficulties, negative results can be defined and evaluated in some circumstances. McClain, Moulton and Sanderson (1999) evaluated the probability of successful colonizations of islands by 132 species of birds, then considered associations between various aspects of ecology, such as nest site or diet breadth, and sexual dimorphism in plumage with the probability of persistence. While this study did not consider evolution, it quantified the first step that is confronted by any organism that faces directional selection, which is the ability to persist. Lee (1999) evaluated freshwater invasions by the marine copepod *Eurytemora affinis* and recorded the persistence of individual colonies. Finally, Bradshaw (1984) reviewed the association between the frequency of tolerance to heavy metals in normal populations of different plant species and whether or not the species had successfully invaded mine sites. In all such cases, it is possible to consider the differences between those species that succeeded and those that did not to evaluate the ecological circumstances and/or properties of the organism that made

a successful response to directional selection more likely.

Genetics

It is also arguable that the sorts of adaptations represented here are in some way not representative of those that are the main substance of evolution. For example, the adaptations associated with anthropogenic influences are often attributable to genes of large effect and simple allelic replacements (e.g. Macnair, 1991b; Jasieniuk & Maxwell, 1994; Majerus, 1998), while we might imagine that most large-scale restructuring of the phenotype would involve polygenic traits. Phenomena like insecticide resistance often involves one or a few major genes because the target of the insecticide is so specific (e.g., Guillemaud et al., 1998); however even seemingly simple responses to anthropogenic influences may often involve more complex, polygenic adaptations. For example, Lefebvre and Vernet (1991) note that heavy metal tolerance is often accompanied by dwarfism and a tolerance of the low nutrient levels that typify mine tailings. Many of the other adaptations that we summarize here are likely to be polygenic traits. Berthold et al. (1992) argue that extensive physiological changes accompany the evolution of a change in migration behavior in birds. Life history evolution in guppies includes changes in development rate, size at maturity, fecundity, and offspring size (Reznick, Bryga & Endler, 1990), plus is correlated to varying degrees with changes in male coloration, behavior, and a diversity of other traits (Endler, 1995). Beak size evolution in soapberry bugs is correlated with changes in adult morphology (wing and wing muscle development), development rate, fecundity, egg size, host preference, and egg to adult survivorship on host plant (Carroll & Boyd, 1992; Carroll, Dingle & Klassen, 1997; Carroll, Klassen & Dingle, 1998; Carroll, pers. commun.). Adaptation to the London underground by *Culex* mosquitos involves a shift in preferred host, loss of a requirement for a blood meal to produce eggs, change in mating behavior, and a change in reproductive phenology (Byrne & Nichols, 1999). Because of the range of characters and the diversity of species involved, we do not see any compelling reason for not considering these collective results as an unrepresentative sample of character evolution. The fact that the majority of our examples involve complex characters is all the more impressive since the rate of evolution is expected to be slower when traits are complex and are

potentially constrained by genetic interactions (Orr, 2000).

The population biology of contemporary adaptations

Brief bursts of directional selection often happen in the context of sub-divided populations. Evidence for the circumscribed nature of such changes is sometimes recorded in the mosaic nature of local adaptation. For example, Lee (1999) complimented her evaluation of the fitness of freshwater versus marine populations of copepods with genetic analyses that demonstrated that the freshwater populations evolved independently in several different parts of its range. Groman and Pellmyr (2000) use similar methods to show that the shift of yucca moths to new species of yuccas happened at least twice. Carroll and Boyd (1992) found that soapberry bugs shifted to three new species of introduced hosts in different parts of the country and evolved a different constellation of adaptations in each case. Thompson (1998) reviews many similar examples of mosaicism, primarily in plant-insect interactions. Such observations support the view that a species consists of a network of populations, each of which is potentially adapting to the local environment, but is also influenced by all of the processes associated with metapopulation dynamics, which include local extinction and the interaction of gene flow and selection (Hanski et al., 1998).

These episodes of sustained directional selection often occur in populations that are colonizing new environments, be they the result of a deliberate introduction by an investigator, a shift to a newly introduced host plant, or the colonization of a denuded mine site. All such environments may share the common properties of reduced competition and the opportunity for population growth (e.g., MacArthur & Wilson, 1963; Wilson 1965). Progress in theoretical conservation biology provides valuable clues about why such colonizations might be conducive to rapid adaptive evolution. Gomulkiewicz and Holt (1995) evaluated the balance between the rate of population decline caused by a change in the environment and directional selection and the rate of evolutionary response to that selection. The probability of local extinction was influenced by a balance among initial population size, rate of population decline and evolutionary potential. They also defined a critical population size, below which extinction becomes very likely because of demographic stochasticity. They conclude that

“...only mildly affected populations at high natural densities can reasonably be expected to be rescued by evolution in novel environments”. Lande (1998) similarly argued that demographic stochasticity and local extinction are likely barriers to local adaptation. Colonizations may share the property of imposing directional selection and also offer the opportunity for population expansion. Daamgard (1996) argues that Haldane’s (1957) calculation of the cost of natural selection implicitly assumes a stable or declining population size; if the population were subject to density regulation or were expanding, then the conditions for a successful response to natural selection could be met more easily.

Our work on guppies illustrates the potential importance of the relationship between the opportunity for population growth and adaptation (Reznick, Rodd & Nunney, 2001). Guppies were collected from natural populations where they experienced either high or low mortality rates, depending upon the predators that they co-occurred with. They were then introduced into streams that previously lacked guppies, but could still be characterized as high or low mortality rate environments. On five occasions guppies were transplanted from a high to a low mortality rate environment. All five introductions were successful and three populations have adapted to their new local environment (Reznick & Bryga, 1987; Reznick, Bryga & Endler, 1990; Reznick et al., 1997, unpublished observations); the other two have not yet been evaluated. On two occasions, guppies were transplanted from a low to a high mortality rate environment. On both occasions the guppies disappeared within a year. When guppies are moved from a high to a low predation environment, fish that have been selected for rapid development and high fecundity are exposed to reduced mortality rates. When they are transplanted from a low to a high predation environment, then fish with relatively slow development and low fecundity experience an increase in mortality rates. Simulations confirm our observations (Reznick, Rodd & Nunney, 2001), which are that the high to low transplants result in explosive population growth, whereas low to high transplants result in a rapid decline to extinction. The opportunity for population growth was thus associated with rapid local adaptation.

The same sorts of population changes may be associated with anthropogenic influences, in which regions with reduced abundance of target species and possibly reduced diversity become available for colonization from surrounding, unaffected areas. There

is a continuous lottery in which the colonists may or may not be successful, but there is also a continuous potential supply of colonists from these surrounding areas. Here, success will likely depend upon the genetic composition of the initial colonists. For example, the species of plants that successfully colonize mine tailings have sometimes been found to have tolerant individuals in populations found off the mine tailings (Bradshaw, 1984) which provides the necessary preadaptation to establish a beachhead in the new environment.

A small minority of the cited studies deal instead with confined populations that successfully respond to directional selection. The best known and best studied example is the body of work by Peter and Rosemary Grant and their colleagues on the medium ground finch (*Geospiza fortis*) population on Daphne Major (e.g., Gibbs & Grant, 1987; Grant & Grant, 1995). This population came perilously close to extinction in the worst drought year (1976), having been reduced to just 180 individuals. These birds are also known to hybridize with small ground finches (*G. fuliginosa*) (Grant & Grant, 1992; Grant, 1993) that occasionally migrate to the island. On the wet El Niño years, the hybrids are as viable and fertile as the parental species. The exceptional resilience of *G. fortis* may thus be attributable to this constant introgression of genetic variation from *G. fuliginosa*.

Contemporary studies versus the fossil record

If evolution can be so fast, then why does it appear to be so slow in the fossil record? Rate estimates from contemporary studies range from four to seven orders of magnitude higher than those seen in the fossil record (Gingerich, 1983; Reznick et al., 1997). The difference between the two sources and the magnitude of the anomaly is even greater if one considers the source of the rate estimates in the fossil record. Haldane’s original application of the darwin to rates of evolution in the fossil record included mammalian data summarized in Simpson’s *Tempo and Mode in Evolution* (1944). Simpson was well aware of the irregular rates of evolution revealed by the fossil record and chose what Gould and Eldredge (1977, 1993) would consider punctuations to evaluate rates of change. These dramatic differences between Haldane’s estimates of less than 0.1 darwin, as compared to values on the order of 10^3 to 10^4 darwins from contemporary data, are thus based on intervals of rapid change in the fossil record. This anomaly demands an explanation.

There are two categories of explanation for the difference between contemporary studies and the fossil record. One is that organisms do not sustain such high rates of evolution over geologic time because the long-term patterns of selection are not the same as are short-term patterns of selection (Gould, 1980). A second possibility is that organisms cannot sustain the rates of change seen in contemporary studies or that the extent of change via natural selection is limited.

First, there is likely to be discordance between the type of selection associated with contemporary studies and that associated with change in the fossil record. The high rates of change seen in contemporary studies are generally attributable to a discrete change in the environment that imposes directional selection. The magnitude of the change will certainly be limited, with the ever-present alternative being local or global extinction if selection is too intense (Gomulkiewicz & Holt, 1995). The anticipated response to such a change is for the rate of evolution to initially be high, then to decelerate as the organism approaches the new optimum because selection will initially fix alleles of large effect, then ones that have progressively smaller effects on fitness (Orr, 1998). Orr (1988) made no explicit predictions about the time course of such events but, if contemporary studies are a good measure of the early time course, then such single episodes of directional selection would be very brief on a geological time scale and would appear as a small vertical step in the fossil record. If the sustained change in the fossil record is to be explained by directional selection, then it would have to be attributable to a sustained but gentle gradient of change in the environment that persists for thousands to millions of years or by a succession of such brief episodes of directional selection.

A diversity of other factors will contribute to a blurring of the signal left in the fossil record by small bursts of directional selection. A high resolution evaluation of morphological change in the fossil record generally lumps data collected over a time interval of hundreds or thousands of years (e.g., Bell, Baumgartner & Olson, 1985) into a single data point. Such an interval is long in comparison to the tempo of change recorded in contemporary studies and will inevitably obscure brief episodes of directional selection. Fine scale change will be further blurred by the mixing of adjacent layers as strata are formed or other forms of time averaging that are typical and ubiquitous in the process of fossilization (e.g., Flessa, Cutler & Meldahl, 1993). If episodes of directional selection are

interdispersed with intervals of no change or reversals in the direction of selection, then these irregularities will be averaged and will yield a systematic underestimate of the rate of change (Bookstein, Gingerich & Kluge, 1978; Gingerich, 1983). If we were to imagine a fossil record of Galapagos finches, then we would probably see little evidence of change in the long term, in spite of very rapid change on a year to year basis, because the direction of evolution is constantly changing (Gibbs & Grant, 1987). Finally, if directional selection affects only a local population that is in turn subject to local extinction or gene flow with other populations, then such local episodes will be averaged over time and space and hence dampen the rate of evolution by natural selection (Barton & Partridge, 2000).

The best available analyses of change in the fossil record from the perspective of quantitative genetics reveal a prevailing theme of stabilizing selection in spite of the appearance of change over time. Lande (1976), Charlesworth (1984b) and Lynch (1990) analyzed patterns of change in selected groups of organisms on the basis of quantitative genetic models. All three authors concluded that the observed rates of evolution were not distinguishable from rates that could be attained by genetic drift. Charlesworth (1984a) argued that, when changes in the mean value of traits are seen in the fossil record, they can be attributed to a very weak gradient of directional selection imposed on the background of stabilizing selection. An important feature of all three analyses is that they include data sets that would otherwise be perceived of as 'punctuations', or intervals of apparently rapid evolution. The anomaly of apparently rapid change in the fossil record not being significantly different from rates predicted by random processes is attributable to the huge differences in the time scale represented by the fossil record relative to the potential rate of change under contemporary processes.

A second category of explanation for the difference between contemporary studies and the fossil record is that organisms are limited in their capacity for change and that natural selection can only fine tune organisms to small changes in their environment (Gould & Eldredge, 1993). Lynch, Lande and colleagues have evaluated sustainable rates of evolution in the context of conservation biology (e.g., Lynch & Lande, 1993; Burger & Lynch, 1995; Lande & Shannon, 1996). The sustainable rate of evolution is modeled as a balance between the consumption of genetic variation by selection and the genesis of new genetic

variation by mutation. Rate was quantified as standard deviation units per generation, or haldanes (Hendry & Kinnison, 1999) and yields estimates of sustainable rates on the order of 0.01–0.1 haldanes. This figure falls within the range of contemporary studies summarized by Hendry and Kinnison (1999), so it is more in line with contemporary rates than the fossil record.

A different argument against the claim that organisms are limited in their capacity to evolve under conventional selection is to consider the record attained by artificial selection, as done by Darwin in the *Origin of Species*. For example, morphologically distinct domestic dogs appeared in the fossil record approximately 10,000 years ago (Vila et al., 1997). Since that time, the range of average body sizes attained among domestic breeds of dogs has exceeded the range of average body size seen among all of the species in the family Canidae, but falls within the range of body sizes in the order Carnivora. Average weights of domestic dogs vary from 1 to 2 kg in Chihuahuas to approximately 80 kg in mastiffs. The Canidae range from 1 to 28 kg, as species averages, while the Carnivora range from less than 0.1 to over 300 kg (Eisenberg, 1981). Similar examples are readily available for many other domestic breeds. This means that an interval of artificial selection that is very brief relative to the fossil record has been sufficient to generate variation that falls between the taxonomic level of family and order. These comparisons are not intended as a model for the process of natural selection, but rather as a model for the capacity of organisms to evolve. They suggest that the response to selection is hardly limited to fine tuning, as has often been claimed (e.g., Gould & Eldredge, 1993).

None of these arguments establish whether or not natural selection actually accounts for the patterns of change seen in the fossil record. They suggest instead that the patterns of change revealed in the fossil record are not inconsistent with what can be attained by natural selection because a diversity of well-understood processes can account for the lack of concordance in rates of evolution. Furthermore, these arguments militate against looking towards the fossil record as a way of evaluating the mechanisms of evolution. Specifically, the fossil record does not provide any arguments for eliminating natural selection as a candidate mechanism. They also suggest that it would be more productive to focus on different questions that address the potential relationship between micro- and macroevolution in a fashion that is more amenable

to empirical investigation. Such questions include a continued evaluation of the sustainable rate of change or on organisms' capacity for change or on the relationship between adaptation and speciation (e.g., Schluter, 1998). All of these questions are already being addressed and there already has been substantial progress in answering them.

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