

Michael T. Kinnison · Andrew P. Hendry
Craig A. Stockwell

Contemporary evolution meets conservation biology II: impediments to integration and application

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Abstract Conservation biology needs to be concerned not just with exogenous threats to populations, but also with the changing nature of populations themselves. In a previous review paper, we highlighted evolution in contemporary time (years to decades) as a largely overlooked aspect of population responses to environmental perturbations. We argued that these responses might affect the fate of natural, managed and exotic populations. In the present review, we discuss issues that may limit the integration of contemporary evolution into conservation biology—with the intent that recognition of these limitations may foster research, discussion and resolution. In particular, we consider (1) alternative perceptions of “evolutionary” and “ecological” time, (2) the role of contemporary evolution as an ecological process, (3) fitness as a bridge between evolution and conservation, and (4) challenges faced by conservation strategies based on gene flow estimation or manipulation. We close by highlighting some situations in which current conservation approaches and contemporary evolution may require reconciliation.

Keywords Rapid evolution · Adaptation · Eco-evolutionary dynamics · Gene flow · Extinction

M. T. Kinnison (✉)
School of Biology and Ecology, University of Maine,
Orono, ME 04469, USA
E-mail: michael.kinnison@umit.maine.edu
Tel.: +1-207-5812575
Fax: +1-207-5812537

A. P. Hendry
Redpath Museum and Department of Biology,
McGill University, Montreal, QC, Canada PQ H3A 2K6

C. A. Stockwell
Department of Biological Sciences,
North Dakota State University,
Fargo, ND 58105, USA

Introduction

Conservation biology is like medicine in that current inaction may often set the stage for future catastrophe. In these crisis-driven fields, attention to acute problems, even triage, is often necessary—although the ultimate goal is to foster rehabilitation and prevent future problems (Soulé 1985). So how do we best achieve these goals? Imagine if doctors considered patients as static bags of flesh and bones, ignoring the dynamic nature of a patient's own contributions to recovery or demise. Imagine too that medicine had turned a blind eye to antibiotic resistance and the origins of novel pathogenic diseases. These short-sighted approaches would obviously have hampered our ability to treat human health problems. And yet, conservation biology might be considered to have treated its patients in much this fashion, typically ignoring natural selection and the ability of populations to evolve in contemporary time.

Most biologists would agree that effective conservation should seek to preserve the systems and processes upon which biodiversity depends, and adaptive evolution surely ranks among these processes (Soulé 1985; Smith et al. 1993). Indeed, conservation biology has important roots in evolutionary biology (Schoenwald-Cox et al. 1983; Soulé 1985), with early leaders emphasizing an evolutionary approach to defining conservation units. Conservation biologists have also been very progressive in integrating new molecular approaches for assessing genetic variation. Most of this work has focused on phylogeny reconstruction for identifying distinct conservation units (e.g., Ryder 1986; Moritz 1994; Avise and Hamrick 1996), or on the genetic health of depleted populations (reviewed by: Lande 1988; Hedrick and Kalinowski 2000; Frankham 2005). The latter concern has stimulated considerable debate regarding the relative importance of genetic versus demographic challenges to population persistence (Lande 1988; Caughley 1994; Hedrick et al. 1996). Poorly represented in this debate has

been the idea that ongoing selection and adaptive evolution may be important for population persistence on contemporary time scales (i.e., years to decades).

In 2003, we wrote a paper highlighting the relevance of contemporary evolution to understanding the fate of indigenous and exotic populations (Stockwell et al. 2003). This review generated considerable interest (over 100 citations in the following 4 years) and has been followed by similar reviews (e.g., Ashley et al. 2003; Ferriere et al. 2004; Lambrinos 2004; Stockwell et al. 2006). Despite this expanding interest, contemporary evolution continues to be a distant, at best secondary, concern in most conservation programs. To some it may even seem like “fiddling while Rome burns.” However, we believe omission of contemporary evolution may come closer to fanning the flames.

Our objective in the present paper is to highlight some perceptual, informational and logistical impediments that surround the incorporation of contemporary evolution into conservation biology—particularly as relates to population decline and recovery. It is perhaps too early to yet to offer sweeping prescriptions for conservation in practice. Nonetheless, we hope that our consideration of impediments will challenge scientists and practitioners to engage in the debates and research needed for balanced and practical integration of contemporary evolution and conservation biology.

Perceptions of evolutionary versus ecological time scales

Evolution has traditionally been considered almost synonymous with long time scales—probably because early authorities were especially concerned with the origins of diversity at the species level and above (Darwin 1859; Simpson 1944). The study of ecology, in contrast, began with problems that were readily observed in contemporary time, such as population growth (Malthus 1798), epidemiology (Ross 1911) and the compositional change of communities (Cowles 1899). The result of these different historical antecedents has been the long-standing distinction between “evolutionary” and “ecological” time. That is, evolutionary processes have been considered to play out over millennia, whereas ecological dynamics occur over days to centuries (Slobodkin 1961; Pianka 2000).

This traditional distinction between evolutionary and ecological time is artificial. Ecology obviously has a long-term component (e.g., Morris et al. 1995), and examples of evolutionary change over contemporary time (Fig. 1) have become increasingly common in the last few decades (reviewed by: Bone and Farres 2001; Kinnison and Hendry 2001; Stockwell et al. 2003). Moreover, such evolution is often associated with the same anthropogenic perturbations (e.g., habitat disturbance, invasions) that drive the current extinction crisis (Stockwell et al. 2003; Hendry et al. 2007). Whereas early studies were often heralded as examples of exceptionally “rapid” evolution, compilations of such studies

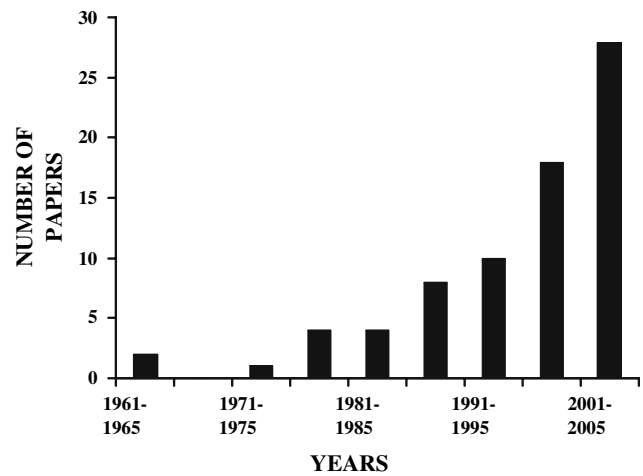


Fig. 1 Increasing abundance of studies of contemporary evolution in the wild (1961–2005). The set of studies portrayed is not comprehensive, but depicts select cases from animal taxa for which the authors have estimated evolutionary rates (data from Hendry et al. 2007; available from APH upon request)

have revealed that rates scale negatively with time; hence, faster rates are thus often expected over short time frames (Gingerich 1983; Thompson 1998; Hendry and Kinnison 1999; Kinnison and Hendry 2001). Thus, it is most appropriate to restrict the term “rapid evolution” to those cases of contemporary evolution that are demonstrably fast relative to others on similar time frames (Hendry and Kinnison 1999). Continued use of the phrase “rapid evolution” for all cases of contemporary evolution fosters the idea that such evolution is the exception when it is likely more the rule.

Conservation biologists should now recognize that the world around us is abuzz with contemporary evolution, often driven by the action of humans. Until this recognition spreads, the temptation will persist to dismiss the role of ongoing evolution in applied ecological contexts.

Evolution as an ecological process

Ecology is widely recognized as a driver of contemporary evolution (e.g., Reznick and Ghalambor 2001), but the converse has received far less attention. In the 1990s, theoretical models (e.g., Gomulkiewicz and Holt 1995) and a review by Thompson (1998) brought renewed interest to the idea that contemporary adaptive evolution may influence ecological outcomes (Hairston Jr. et al. 2005; Bailey et al. 2006; Fussman et al. 2007; Kinnison and Hairston Jr. 2007). In other words, the dynamics of populations, communities and ecosystems are potentially *eco-evolutionary*, not just ecological.

So why has contemporary evolution been slower to gain steam in conservation biology than in ecology as a whole? Reasons are likely varied, but three are probably widely influential. First, conservation biologists may

often presume that population declines are primarily a problem of habitat loss, interactions with invaders, or exploitation, and not maladaptation. Second, evolutionary considerations may be perceived as superfluous when populations are already critically depleted and vulnerable to demographic stochasticity and genetic deterioration (Lande 1988; Amos and Balmford 2001). Finally, some conservation practitioners may believe that their focal organisms are unlikely to show contemporary evolution because of various life history features, such as long generation times (Myers and Knoll 2001). Each of these views may be true to some degree, but each deserves more refined consideration.

Populations may often decline due to the immediate demographic consequences of habitat loss, interactions with invaders or exploitation, but these forces are also likely drivers of selection and contemporary evolution. For example, the harvesting of wild plants and animals is notoriously selective, and the resulting trait evolution may even impede subsequent recovery (Olsen et al. 2004; Law and Salick 2005). Habitat fragmentation and loss may lead to selection on dispersal tendencies or the use of alternate resources, and native species can evolve novel interactions in response to invaders. Fitting with such selection, a number of phytophagous insect species have adapted to use introduced plants (e.g., Carroll et al. 1998) and Australian snakes have evolved means to cope with toxins of introduced cane toads (Phillips and Shine 2004). The indirect demographic costs and benefits of evolutionary limitations and responses need to be weighed alongside the direct demographic effects of habitat loss and exploitation.

We should also not forget that strict density-regulation associated with habitat or resource limitation is not universal. Many organisms manifest strong population cycles (e.g., predator-prey) or complicated metapopulation dynamics. Recent studies suggest that population dynamics in such species may be strongly influenced by genetic variation and contemporary evolution (Yoshida et al. 2003; Hanski and Saccheri 2006). For instance, Yoshida et al. (2003) showed that the presence or absence of genetic variation in prey (alga) influences the periodicity of cycles with predators (rotifers) in chemostats. Such evolution can theoretically stabilize cycles in a way that reduces the risk of extinction (Johnson and Agrawal 2003). Alternatively, the potential for contemporary co-evolution raises the possibility that some species declines are abetted by evolution in competitors or predators (including exotic invaders).

For populations in an acute state of demographic or genetic jeopardy by dint of maladaptation (e.g., Gomulkiewicz and Holt 1995; Boulding and Hay 2001), ignoring the role of contemporary evolution is akin to treating the symptoms of disease while ignoring the causal agent. Such populations will never recover in the wild unless maladaptation is addressed. However, even modest improvements in adaptation might theoretically invert a demographic and genetic “vortex of extinc-

tion” (Gilpin and Soulé 1986) into a “vortex of persistence” (Kinnison and Hairston Jr. 2007). In this latter vortex, positive population growth resulting from adaptation is expected to: (1) quickly limit some of the acute threats of small population sizes (e.g., demographic stochasticity, allee effects and genetic drift), (2) increase population capacities to purge genetic loads (introduced by mutation, inbreeding and gene flow) and (3) favor odds that beneficial genotypes will arise and be retained by selection. As a result, further adaptation may become more efficient with added contributions to population fitness, growth and persistence.

Although it is certainly true that some species evolve more slowly on an absolute time scale, by virtue of their life history features, this does not mean that contemporary evolution is irrelevant to those species. Organisms may experience appreciable selection and shifts in genotype frequencies within a single generation (e.g., Grant and Grant 1995). Moreover, organisms with features that slow their evolution may especially benefit from conservation approaches that more directly seek to foster it. For example, the selective breeding of disease-resistant trees, such as American elms (*Ulmus americana*), suggests that human-aided adaptive evolution may offer hope for some extremely long-lived species (Snieszko 2006).

But is evolution as an ecological process important enough to really command our practical attention? Recent heuristic analyses suggest that it can be. In particular, Hairston et al. (2005) showed that annual population growth rates in Darwin’s finches are more than twice as strongly affected by adaptive changes in beak size as they are by ecological changes in food availability. Even this example may underestimate the full potential of contemporary evolution given that it only considers changes in beak and body dimensions. What of the combined fitness effects of contemporary evolution integrated over all traits constituting a phenotype? We now turn to this topic.

Evolution of fitness: beyond traits

Studies of contemporary evolution typically focus on a few traits with expected contributions to overall fitness. But population persistence and recovery will be a function of changes in overall fitness, which is determined by all traits that influence fitness. Unfortunately, evolutionary biologists know exceedingly little about the evolution of major fitness components in natural populations facing environmental change. We suggest that empirical studies of contemporary evolution need to turn from an exclusive emphasis on particular traits to a more inclusive analysis of changes in major fitness components.

Fisher (1930) argued that natural selection perpetually increases mean fitness in a population, whereas various aspects of environmental deterioration, many

wrought by the population itself (e.g., competition), decrease it. The interaction between these forces then generates a dynamic equilibrium wherein realized fitness and population growth are held close to replacement through time (Price 1972; Burt 1995). When this equilibrium is perturbed by some environmental change, mean fitness may fall below replacement. However, natural selection is expected to improve mean fitness until an equilibrium is again approached. The question is whether this increase can come rapidly enough to offset the demographic costs of environmental deterioration.

Of course, measuring fitness is a tricky prospect, in part because biologists have difficulty even agreeing on what constitutes “fitness” (Ariew and Lewontin 2004). It is nonetheless possible to measure major components of fitness, such as the vital rates of survival and reproduction. These performance metrics implicitly integrate over many aspects of the phenotype and life history of an organism, and thus provide a more inclusive picture of contemporary adaptation. A few studies of laboratory populations have assessed the evolution of such fitness metrics by introducing populations into new environments and then later competing the ancestral and descendent populations in that environment. These studies typically find that fitness can change substantially in as short as a few generations (Travisano et al. 1995; Gilligan and Frankham 2003).

An analogous approach can be applied to at least some wild systems, particularly those in which populations are introduced to new environments and then compared to their ancestral sources, or one another in the wild. The only two studies that we know to have adopted this approach are our own on introduced Chinook salmon (*Oncorhynchus tshawytscha*) and Trinidadian guppies (*Poecilia reticulata*). Both studies demonstrate that contemporary evolution can dramatically improve survival or reproductive rates in only 20–30 generations (Kinnison et al. 2007; Gordon et al., in review). The greatest changes were observed for Chinook salmon, for which adaptation to a new river more than doubled survival and total egg production. On the flip side, a number of studies provide evidence that populations can suffer substantial fitness tradeoffs in the wild in association with adaptation to captive rearing environments (see below). In short, contemporary evolution likely changes overall fitness in the wild, the parameter we really care about, much more rapidly than it changes individual phenotypic traits.

We recognize that the above experimental approaches are not practical in many conservation contexts, except perhaps in the field of restoration ecology (Stockwell et al. 2006). Nonetheless, more such studies are needed if we are to foster a functional appreciation of the scope of contemporary evolution to aid population persistence and recovery under various conditions. We suspect that the resulting insights may cause even

recalcitrant conservation practitioners to re-evaluate where evolution sits among their list of priorities.

Dispersal and gene flow: what do we really know?

Conservation biologists are often forced to consider the implications of movement across landscapes by organisms (dispersal) and their genes (gene flow). Much of this work was initially motivated by the need to identify population units for management (e.g., Waples 1995; Avise and Hamrick 1996). Increasingly, however, focus has shifted to how human actions can decrease or increase movement, and to how these changes might influence the genetic and demographic health of populations. We believe that the sparse information on these topics is a critical impediment to evolutionarily informed conservation biology, and so we mount our soap box to provide some insights into the challenges at hand.

Dispersal and gene flow can have several positive effects on adaptation and population persistence. First, gene flow can reduce inbreeding and help mask recessive deleterious mutations (Hedrick 1995; Hogg et al. 2006). Second, gene flow can increase the genetic variation available for adaptation to changing conditions (Swindell and Bouzat 2006). Third, gene flow can dampen stochastic variation owing to genetic drift in small populations, and thereby increase mean fitness across the range of a species (Alleaume-Benharira et al. 2006). Even without these *genetic* effects, dispersal can have positive demographic influences that feed back on adaptation. In particular, dispersal can sometimes maintain sink populations for long enough that they can begin to adapt to local conditions (Holt and Gomulkiewicz 1997; Holt et al. 2003).

Dispersal and gene flow can also have several negative effects on adaptation and population persistence. First, gene flow reduces the genetic independence of populations, and can thereby reduce adaptive divergence (Darwin 1859; Garcia-Ramos and Kirkpatrick 1997; Lenormand 2002; Moore et al. 2007). If this lack of independence introduces enough of a genetic load then it can hamper population responses to environmental change (e.g., Gomulkiewicz et al. 1999; Boulding and Hay 2001) and set limits to species ranges (reviewed by: Bridle and Vines 2007). Second, dispersal, even without resulting gene flow, may sometimes increase local population densities to the point that carrying capacities are exceeded and depress the fitness of local genotypes (Gomulkiewicz et al. 1999).

These intriguing but obfuscating complexities suggest the need to empirically disentangle the multifarious influences of gene flow on adaptive evolution (Garant et al. 2007). Full integration will likely take some time and, in the interim, we provide some cautionary reminders about interpreting dispersal and gene flow in the context of contemporary evolution and conservation.

1. Gene flow will rarely prevent local adaptation, and natural selection will rarely overwhelm gene flow. Instead, adaptive divergence represents a dynamic balance between the two forces, such that most populations will be partly adapted and at the same time partly constrained (Hendry et al. 2001; Garant et al. 2007).
2. Dispersal and gene flow are unlikely to be equal. Gene flow can be higher than dispersal owing to heterosis when populations are inbred (e.g., Ebert et al. 2002), or gene flow can be lower than dispersal in the case of selection against immigrants and hybrids (e.g., Hendry et al. 2000).
3. Dispersing individuals are not always a random subset of their source population. This non-random dispersal can substantially influence the dynamics of colonization, adaptive divergence and population persistence (Quinn et al. 2001; Garant et al. 2005; Hanski and Saccheri 2006).
4. Unlike neutral loci, constraints on adaptive divergence are more directly related to the proportion of immigrants (m) than to their absolute number (Nm) (Holt and Gomulkiewicz 1997; Hendry et al. 2001). Because of this, the fitness consequences of a given number of immigrants will vary with local population size (N). Human-mediated manipulations of dispersal should be implemented with this in mind (Hedrick 1995).
5. Rates of gene flow estimated from neutral loci represent effective introgression for those markers. They do not tell us how selection may have acted on the larger migrant pool to restrict the features of successful migrants and rates of introgression at selected loci (Garant et al. 2007). Hence, such estimates are likely insufficient for establishing rates of population mixing in captivity.

In summary, dispersal and gene flow can have a bewildering array of both positive and negative impacts on threatened populations, making both prediction and manipulation a tricky prospect. Although some studies have attempted to determine “optimal” dispersal rates in a conservation context (Hedrick 1995), the costs and benefits of dispersal manipulations are not clear (e.g., Storfer 1999; Tallmon 2004). Much more research needs to be done to make gene flow a reliable tool for eco-evolutionary conservation.

Reconciling the old and the new

Given that populations are expected to evolve in response to natural and anthropogenic perturbations, it is appropriate that practitioners seek eco-evolutionary solutions to conservation problems. We are not saying this will be easy. Particularly challenging is the problem that some current conservation approaches may be at odds with optimal considerations from the perspective of contemporary evolution. Here, we briefly outline two

areas of conflict that have begun to draw attention—captive propagation and refuge populations.

Captive propagation for reintroduction is a necessary last line of defense for many threatened species. Unfortunately, populations brought under captive propagation are likely to quickly adapt to those conditions (Heath et al. 2003; Schuster et al. 2005), with adaptation to the natural environment decreasing as a byproduct (Reisenbichler and Rubin 1999; Woodworth et al. 2002). Such domestication selection can occur even when managers actively try to prevent it (McLean et al. 2005). Particularly insidious, rearing programs are specifically designed to reduce mortality on some life stages, which means that they can shift the balance of direct and indirect selection acting on traits and foster drift. Resulting evolutionary changes away from the well-adapted natural condition may then be expected to impair the fitness of the propagated population and of wild populations where interbreeding occurs (Gilligan and Frankham 2003; Heath et al. 2003).

Less appreciated, the evolutionary effects of captive propagation do not end at the doors of the production facility. Where rearing programs release individuals under unnatural conditions or environmentally alter natural phenotypes or behaviors (i.e., phenotypic plasticity), natural selection in the wild could result in unnatural patterns of genotypic evolution. For example, genotypes that are released at the wrong time or stage may face unnatural selection on phenology-related traits. Once in the wild, captive-reared individuals might also change selection acting on wild populations through direct and indirect interactions (e.g., competition or predator functional responses).

Reducing the environmental and selective differences between captive and wild environments would reduce some of the above concerns, but could entail a reduction in the demographic boost that is usually targeted by captive propagation. Current methods from evolutionary biology for measuring natural selection could provide tools for comparing selection on propagated and naturally produced individuals in the wild to reduce selective disparities. The best solution, of course, would be to minimize the initial need for captive propagation, perhaps by addressing evolutionary concerns before populations collapse.

The establishment of “refuge” populations in the wild represents a current alternative to captive propagation. The problem here is that refuge environments will rarely be identical to the ancestral environment and, like most introductions and invasions adaptive divergence is thus generally expected (Stockwell and Weeks 1999; Collyer et al. 2005). Refuge populations also may be vulnerable to genetic drift and founding events (Stockwell et al. 1996). Both of these effects are exemplified by recently established populations of the western mosquitofish (*Gambusia affinis*), wherein introduced populations lost considerable genetic diversity (Stockwell et al. 1996) and underwent substantial

life history evolution (Stockwell and Weeks 1999). Changes such as these likely reduce the value of refuge populations for use in supplementing original ancestral sources. Disastrous outcomes from such supplementation might be reduced by assessing divergence and selective disparities in refuge populations before individuals are returned to the ancestral site in substantial numbers.

The above concerns hint at fundamental questions regarding the operational goals of conservation programs. Aside from demographic persistence, current conservation efforts emphasize the preservation or rehabilitation of genetic variation. And yet these goals are not always compatible with fostering current adaptation (Stockwell et al. 2003, 2006). In particular, programs that seek to maintain genetic variation often take great measures to shield populations from selective mortality and to increase effective population size. Adaptation, however, entails (1) the selective loss of genetic variation, (2) unequal contributions by different individuals to future generations, (3) increased inbreeding among the offspring of individuals with higher fitness and (4) an initial reduction in effective population size. We suggest that the preservation of genetic variation for an abstract future should not necessarily supersede adaptive evolution to the tangible present (Stockwell et al. 2006). New ways to balance these goals should be a central research theme of an eco-evolutionary approach to conservation (e.g., Schaeffer et al. 2005; Stockwell et al. 2006).

Summary

The time scales of ecology and evolution are fully entwined, and the tremendous potential for adaptive evolution in contemporary time has prompted growing interest in the ways that such evolution might influence the dynamics of populations, communities and ecosystems. We hope that conservation biologists will recast the problems of their field in an eco-evolutionary context (Kinnison and Hairston Jr. 2007), with the recognition that this new direction may require revision of some current conservation objectives and strategies. Evolutionary biologists can still do much to pave the way for this transition. Impediments aside, contemporary evolution is likely a factor in population persistence, and our ability to accommodate it could be the difference between conservation as triage, and conservation as prevention and recovery.

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