



Review

Evolutionarily enlightened management

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Received 27 September 2001; received in revised form 15 July 2002; accepted 30 August 2002

Abstract

Here we review growing evidence that microevolutionary changes may often be rapid and, in many cases, occur on time frames comparable to human disturbance and anthropogenic change. Contemporary evolutionary change has been documented in relatively pristine habitats, in disturbed populations, under captive management, and in association with both intentional and inadvertent introductions. We argue that evolutionary thinking is thus relevant to conservation biology and resource management but has received insufficient consideration. Ignoring evolution may have a variety of consequences, including unpredicted evolutionary responses to disturbance and naive or inappropriate management decisions. Philosophically, we must also grapple with the issue of whether the evolution of adaptations to disturbance and degraded habitats is sometimes beneficial or something to be rigorously avoided. We advocate promoting *evolutionarily enlightened management* [Lecture Notes in Biomathematics 99 (1994) 248], in which both the ecological and evolutionary consequences of resource management decisions are considered.

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Keywords: Microevolution; Rapid evolution; Evolutionarily enlightened management; Conservation

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1. Introduction

Anthropogenic effects are now seen in every ecosystem on earth, and humans dominate many ecosystems

(Vitousek et al., 1997). Native habitats are being lost and fragmented at alarming rates, and more and more biological resources will require human intervention and management in order to persist. Stemming the tide of extinctions due to habitat loss, introduction of alien species, and overexploitation should and must continue to be urgent goals. We advocate *evolutionarily enlightened management* to help advance these goals. When

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harvesting, managing or conserving species, evolutionarily enlightened management occurs when both the ecological and evolutionary consequences of management decisions are considered. In particular, there is a need to increasingly recognize, understand, and consider the *evolutionary* correlates of anthropogenic forces in conservation biology. In the face of environmental change, species must either respond to the selective pressures imposed by the environment or ultimately be lost to extinction. Implicit in most conservationist thinking is that human disturbance occurs at rates so rapid that the glacially slow process of adaptation through natural selection cannot occur, and therefore evolutionary change is of minor importance in our quest to preserve biodiversity. Yet there is growing evidence that evolutionary shifts are sometimes very rapid and are probably changing many of the species we are trying to protect.

2. Evidence for rapid evolution

The term “microevolution” is generally used to refer to changes that take place within species and populations within the approximate lifespan of a human being (Dobzhansky, 1941, p. 12; Hendry and Kinnison, 1999). Measurable microevolutionary change has often been observable over periods of years or even months (Gingerich, 1993; Thompson, 1998; Hendry and Kinnison, 1999). In a classic study of Galapagos finches (*Geospiza fortis*), increases in body and beak size occurred in response to a single episode of selection brought on by drought conditions (Boag and Grant, 1981), a trend that was later reversed during an El Niño event (Gibbs and Grant, 1987; Grant and Grant, 1995). In the case of three subspecies of Channel Island deer mice (*Peromyscus maniculatus*), changes in external and cranial measurements as great as 10% were documented in museum specimens collected over less than 90 years (Pergams and Ashley, 1999). This case was an accidental discovery and the selective agent is not known; perhaps

many cases of microevolution are never documented. Other examples of rapid evolution not obviously or directly tied to anthropogenic factors are given in Table 1, although human activity likely played an indirect role in some of these cases.

Although rapid evolutionary change has been documented in “undisturbed” systems, the vast majority of cases of microevolutionary change in contemporary populations involve human disturbance or activity. Table 2 provides a few such examples to illustrate the taxonomic breadth and diversity of selective responses; more thorough reviews can be found in Hendry and Kinnison (1999), Bone and Farres (2001), Kinnison and Hendry (2001), and Reznick and Ghalambor (2001). In a review of documented cases of contemporary microevolution, 18 (86%) of the 21 cases listed (Hendry and Kinnison, 1999; Table 1) involved anthropogenic causes. In particular, colonization events and the establishment of populations in novel environments are most often associated with rapid evolutionary events (Reznick and Ghalambor, 2001). Examples include molecular and morphological change reported in house mice since their introductions to small islands off the British coast within the past two centuries (Berry, 1964; 1986; Berry et al., 1978) and in rats introduced to the Galapagos Islands (Patton et al., 1975; Pergams and Ashley, 2001). North American house sparrows evolved rapidly following their haphazard introduction from Europe (Johnston and Selander, 1964) and a geographic cline in wing size has apparently “re-evolved” in introduced North America populations of the European fruit fly *Drosophila subobscura* in just two decades (Huey et al., 2000; Gilchrist et al., 2001). Rapid adaptive responses have also been documented in behavioral traits following introduction, such as migratory behavior (Berthold et al., 1992; Able and Belthoff, 1998) and ability to escape from predators (Magurran et al., 1992; O’Steen et al., 2002).

Introduction of fish into new habitats has been shown to alter selection on a variety of traits. Introduced

Table 1
Examples of rapid evolution responses to non-anthropogenic agents

Species	Citation	Selective agent	Trait(s) responding	Time frame
<i>Petrochelidon pyrrhonota</i> (cliff swallows)	Brown and Brown, 1998	Cold, wet weather	Body size, asymmetry	6 days
<i>Peromyscus maniculatus</i> (Channel Island deer mice)	Pergams and Ashley, 1999	Unknown	Cranial characters, body size	90 years
<i>Geospiza fortis</i> (Galapagos finches)	Boag and Grant, 1981	Drought	Body and beak size	Single season
<i>Hypochaeris radicata</i> , <i>Lactucua muralis</i> , <i>Senecio sylvaticus</i>	Cody and Overton, 1996	Natural island colonization	Seed dispersal ability	Five generations
<i>Carpodacus mexicanus</i> (house finch)	Badyaev et al., 2000	Range expansion	Sexual dimorphism	<50 years

populations of the endangered White Sands pupfish exhibited significant shifts in allele frequencies at an allozyme locus associated with salinity in less than 30 years (Stockwell and Mulvey, 1998). Nonnative sockeye salmon (*Oncorhynchus nerka*) show rapid divergence of male and female body size and male body depth in accordance with stream size (Hendry and Quinn, 1997). Reproductive isolation (Hendry et al., 2000) and adaptive divergence in hatching time (Hendry et al., 1998) have evolved in less than 15 generations in other populations of sockeye salmon. Ninety years after introduction to rivers in New Zealand, chinook salmon (*Oncorhynchus tshawytscha*) have diverged in morphology, gonadal investment, reproductive timing and growth rate (Kinison et al., 1998a, b; Quinn et al., 2000).

Rapid evolutionary responses can be seen not only in introduced species, but also in native species interacting with alien species. The soapberry bug (*Jadera haematoloma*) has evolved different and appropriate beak lengths as it shifted to different introduced host plants over periods of less than 50 years (Carroll and Boyd 1992; Carroll et al. 1997). Similarly, population of yucca

moths (*Prodoxus quinquepunctellus*) rapidly shifted emergence time and ovipositor morphology following colonization of a new host species (Groman and Pellmyr, 2000). Extinctions as well as introductions can result in microevolution. Extinctions of their food sources (lobelioid plants having long decurved corollas) apparently resulted in a change in mandible length in the Hawaiian honeycreeper (*Vestiaria coccinia*) over the last century (Smith et al., 1995).

Fisheries have been described as large-scale experiments on life history evolution (Rijnsdorp, 1993), and are, not surprisingly, rich in examples of human-induced microevolution (reviewed in Law, 2000). For example, heavy harvesting of Pacific salmon (often >75% of a population returning to spawning streams; Rogers, 1987; Labelle et al., 1997) severely alters selection on life history traits (Hendry and Kinison, 1999). By differentially removing larger fish from harvested populations, gill netting exerts intense selection on age and size at sexual maturity, and predicted response to harvesting practices have been reported for many fish stocks (Ricker, 1981; Healey, 1986; Nelson

Table 2
Examples of rapid evolutionary responses to anthropogenic agents

Species	Citation	Selective agent	Trait(s) responding	Time frame
Invertebrates				
> 70 species	Kettlewell, 1973	Industrial pollution	Melanism	< 100 years
<i>Culex pipiens</i> (mosquito)	Bryne and Nichols, 1999	Colonization of London underground	Mating behavior, reproductive phenology, preferred host, etc.	< 100 years
<i>Drosophila subobscura</i>	Gilchrist et al., 2001	Introduction to North America	Latitudinal wing size clines	< 20 years
<i>Jadera haematoloma</i> (soapberry bug)	Carroll and Boyd, 1992; Carroll et al., 1997	Introduced host plants	Beak length	< 50 years
<i>Eurytemora affinis</i> (marine copepod)	Lee, 1999	Colonization of freshwater habitat	Physiological traits	< 20 years
Plants				
> 10 species	reviewed in Bone and Farres, 2001	Mining	Heavy metal tolerance (zinc, copper, lead)	< 150 years
<i>Arabidopsis thaliana</i>	Ward et al., 2000	High CO ₂	Seed production	< 1 year
<i>Plantago major</i>	Davison and Reiling, 1995	High ozone	Growth rate	6 years
Vertebrates				
<i>Poecilia reticulata</i> (Trinidadian guppies)	O'Steen et al., 2002	Introduction to high-predation environment	Escape ability	26–36 generations
<i>Oncorhynchus tshawytscha</i> (Chinook salmon)	reviewed in Quinn et al., 2001	Introduction to New Zealand	Behavioral, physiological and life history traits	30 generations
<i>Anolis carolinensis</i> , <i>A. sagrei</i> (Anolis lizards)	Losos et al., 2001	Experimental introduction to small islands	Body shape, hind limb length	< 15 years
<i>Carpodacus mexicanus</i> (house finch)	Able and Belthoff, 1998	Introduction	Migratory behavior	20 years
<i>Vestiaria coccinia</i> (Hawaiian honeycreeper)	Smith et al., 1995	Extinction of food source	Bill size	< 100 years

and Soulé, 1987; Brown and Parman, 1994, Stokes and Law, 2000). Responses in non-target species taken as by-catch have also been reported (Haugen and Vøllestad, 2001). Harvests directed at early or late portions of salmon runs by human and other predators have been shown to alter run timing, breeding time and sex ratio (Nelson and Soulé, 1987; Quinn and Kinnison, 1999). Severe reduction in spawning density and high mortality of large fish undoubtedly shifts selection pressures on social systems, including patterns of sexual selection (Foote, 1988; Fleming and Gross, 1994; Quinn and Foote, 1994; Willson, 2002) and competition among females for nest sites. While the evolutionary consequences of fish harvests have been noted in the scientific literature for some time (e.g. Adams, 1980; Ricker, 1981), the concept has only recently begun to receive noteworthy consideration (Law, 2000; Browman, 2000).

Examples of rapid microevolution in plants are also numerous (reviewed in Bone and Farres, 2001). Classic studies include the evolution of heavy metal tolerance near mines (Antonovics and Bradshaw, 1970; Wu and Kruckeberg, 1985) and adaptation in elevated pH (Davies and Snaydon, 1976). More recent examples include rapid evolution for resistance to ozone pollution (Davison and Reiling, 1995) and atmospheric CO₂ (Ward et al., 2000). As with animal studies, plant introductions and colonizations also provide many examples of rapid evolution, including changes in resistance to herbivory (Blossey and Nötzold, 1995; Daehler and Strong, 1997) and seed dispersal ability (Cody and Overton, 1996). Many cases of rapid evolution in plants involve perennials (Bone and Farres, 2001) and even long-lived species such as trees (Scholz et al., 1989), so the phenomenon is not limited to herbaceous species with short generation times.

3. Imperative of evolutionarily enlightened management

Ineffective or even detrimental management practices may result when microevolution is not considered. Hatchery programs have been popular attempts to restore profitable harvest levels for many fish stocks. However, hatchery conditions create selection for traits that differ from those favored in wild populations (Allendorf et al., 1987; Berejikian et al., 1996; Johnson et al., 1996; Fleming and Gross, 1989; Reisenbichler, 1997; Unwin and Glova, 1997). Augmentation of native populations with individuals harboring genes advanced by selection in captivity will probably have negative consequences for the management program (Lynch, 1996). In fact, recent theoretical studies suggest that selection in captivity during supportive breeding will likely reduce a wild population's fitness even when wild individuals are continually introduced into the captive population (Lynch and O'Hely, 2001; Ford, 2002).

Microevolutionary considerations have often not been carefully considered during intentional introductions of nonnative species for management purposes. For example, red squirrels (*Tamiasciurus hudsonicus*) have been introduced to several regions in North America (e.g. Burris and McKnight, 1973; Pimm, 1990) in hopes of increasing the availability of prey for the pine marten (*Martes americana*). Squirrels exert significant selection pressures on the cone characteristics of conifer trees (Benkman, 1995), eventually reducing the accessibility of seeds to conifer-seed-eating birds (in addition to the direct competitive effects of reducing seed abundance). In addition, red squirrels are major predators on birds' nests in northern forests (Sieving and Willson, 1998) and might select for changes in nesting habits and life histories.

While habitat fragmentation has been a major focus of conservation research, the evolutionary consequences of fragmentation are often unappreciated. In the face of reduced levels of gene flow among previously connected fragments, differentiation among populations will increase by the evolutionary processes of genetic drift and selection. Substantial genetic differentiation has been reported between urban frog populations separated by less than 3 km (Hitchings and Beebee, 1997). With habitat fragmentation, species experience reduced habitat scales, facilitating selection for adaptation to local conditions. Subdivided populations subjected to heterogeneous environmental conditions (often due to anthropogenic influences) commonly exhibit rapid evolution (Reznick and Ghalamber, 2001). Increased propensity for genetic differentiation and local adaptation (which could be viewed as positive or negative, depending on the situation) are generally not a consideration of resource management. Fragmentation of habitat combined with management efforts may create source/sink dynamics with important correlates for selection. For example, pesky squirrels, raccoons, and skunks are often trapped in residential areas and dumped into nearby nature preserves, setting up a source/sink system with a net positive flow of migrants from residential areas (source populations) to preserves (sinks). Evolutionary theory has demonstrated how this creates selection for specializations to the source habitat, and we therefore inadvertently promote the evolution of urban adaptations by this practice (Brown and Pavlovic, 1992; Holt and Gaines, 1992).

4. Obstacles to evolutionarily enlightened management

Why has evolution been given such a low priority in most resource management programs, academic as well as applied? We suggest that the reasons include the following: (1) typological thinking, the mistaken view that species are relatively fixed entities that remain unchanged

over conservation-relevant periods of time; (2) current conceptual approaches to evolutionary biology that have limited applications in conservation and management; and (3) scientific challenges in assessing and predicting evolutionary forces and their outcomes.

Although most biologists recognize that individual variation is ubiquitous in nature and indeed is the basis for evolutionary change, typological thinking is still pervasive. This view persists in conservation and management because it is usually assumed that evolutionary change is slow or only detectable in species with short generation times. While rapid responses to selection are widely recognized in phenomena such as the evolution of antibiotic and pesticide resistance, it is often thought to apply only to organisms such as bacteria or short-lived parasites and pests, not those that make endangered species lists. The growing number of examples of rapid evolution in long-lived organisms already mentioned here (Tables 1 and 2) indicates that many species respond quickly to new selective pressures, and most of the selective pressures associated with human activity will be extremely strong (Palumbi, 2001). Yet the view that species are relatively homogeneous, fixed entities continues to shape research agendas in many areas of environmental science. For example, in the field of global change research, numerous growth-chamber and open-top chamber experiments have documented potential responses of organisms to variables such as elevated CO₂ and temperature. Predicted changes in climate have also been used to anticipate the expansion and contraction of species ranges (Iverson et al., 1999; Schwartz et al., 2001). Such approaches generally make the assumption that the focal organisms themselves will not adapt to the altered environmental conditions, and thus predictions for the future emerge by simply extrapolation from the existing ecologies of fixed species. In reality, organisms will probably respond both ecologically and evolutionarily. Climate adaptation and impediments to gene flow, not just range shifts, must be considered in climate change models (Davis and Shaw, 2001). Although microevolution in response to climate change has been demonstrated (Rodríguez-Trelles and Rodríguez, 1998; Ward et al., 2000), adaptive responses appear to be outside the mainstream of global change research (Hughes, 2000; Davis and Shaw, 2001; but see Geber and Dawson, 1993).

Approaches in conservation biology such as population viability analysis (PVA) are similarly based on the assumption that species have “static” demographic and life history characteristics that can be used to model the population dynamics of a target species. The utility and accuracy of predictions made using PVA have recently been attacked on several fronts. Criticisms include a lack of (or inappropriate) model validation (McCarthy et al., 2001), inaccuracy in parameter estimation (Beisinger and Westphal, 1998; Ellner et al., 2002) and

overall imprecision (Ludwig, 1999; Fieberg and Ellner, 2000), but evolutionary responses of the modeled species have not been considered. While environmental variation is often incorporated into the model, specific characteristics such as breeding age, litter size, and dispersal rates are fixed throughout the simulation. Interestingly, often PVA is used to assess the probability of persistence of a population for 100 years, which encompasses the time frame documenting evolutionary change in the examples described above.

Second, the two most common conceptual approaches in evolutionary biology, population genetics and phylogenetics, often are not directly applicable to evolutionarily enlightened management. The first conceptual approach lies in the related disciplines of population genetics and quantitative genetics. These fields define evolution as changes in gene frequencies, and evolutionary dynamics and equilibria are projected explicitly. Complete knowledge of the underlying genetics and ecology of a system should succeed in predicting the adaptive response or organisms to altered environments. Unfortunately, the gap between our knowledge of specific genes or quantitative characters and the adaptive responses of organisms is still substantial. Genetic models that attempt to deal with realistic ecological scenarios of temporal and spatial environmental heterogeneity and frequency- and density-dependent fitness will likely be too cumbersome and inaccurate to be useful in the foreseeable future. In fact, the most common applications of population genetics to conservation biology specifically avoid genes that may be under selection. Studies examining stock structure, dispersal and effective population size intentionally employ neutral molecular markers so that the observed population parameters can be explained by a balance between mutation, drift and gene flow without the complicating effects of selection. While such markers are useful for assessing population subdivision, they may be quite poor predictors of the evolutionary potential of populations. Recent studies indicate that commonly used molecular markers such as allozymes and microsatellites are inadequate indicators of ecologically important quantitative genetic variation (Podolsky, 2000; Morgan et al., 2001; Reed and Frankham, 2001). Unfortunately, the vast majority of population genetic information available for endangered species is for neutral molecular markers, not for quantitative characters upon which selection can act (Frankham, 1995).

The other major thrust of evolutionary research is historical research programs involving systematics and phylogenetics. These approaches provide an empirical reconstruction of the pattern of evolution through time and have aided in identifying the origins, uniqueness, and position of taxa of conservation interest and been used to set priorities for conservation (e.g. Parnell, 1995; Faith 1996; Soltis and Gitzendanner, 1999). Yet

phylogenetic approaches provide little information for evolutionarily enlightened management. In selecting traits for phylogenetic studies, rapidly evolving traits that may respond quickly to changing selection pressures are disregarded because of their tendency to exhibit homoplasy. Construction of phylogenetic trees provides a hierarchy of character states but do not specify the evolutionary forces responsible for producing or maintaining those states. Lastly, the phylogenetic approach implicitly assumes that phylogenetic constraints play a bigger role than adaptive evolution. Together, these features of phylogenetics encourage the view that much adaptive evolution cannot happen or that it will happen very slowly or sporadically.

Finally, ecological and evolutionary interactions are complex, making it difficult to predict the outcome of changes in selection in particular populations (Abrams, 1996) in the absence of detailed knowledge (Grant and Grant, 1995). Our ignorance of the patterns and intensity of selection in particular natural populations generally impedes our ability to predict outcomes and to either avoid or utilize particular consequences of altered selection pressures. Orians (1998) has highlighted the eclipse of natural selection in ecology and, at the 2000 meeting of the Ecological Society of America, linking evolution with ecology was seen as one of the greatest challenges facing ecologists. The crossovers between “evolution” meetings, “ecology” meetings and “conservation and management” meetings are embarrassingly few. Successful application of evolutionary thinking to conservation will require an evolutionary approach that emphasizes the interplay between adaptive evolution and its ecological consequences and origins.

5. Recommendations

What can be done to promote evolutionarily enlightened management? We can take active steps. Current approaches to conservation and management strive to be ecologically enlightened by evaluating the ecological consequences embodied in human disturbances and management plans. An evolutionarily enlightened manager can ask what are the evolutionary as well as the ecological implications of human activity and management actions. Managers can focus attention on the evolutionary context of a species and its traits, consider whether certain attributes of the species are ecologically valuable (e.g. anti-predator behaviors and morphologies that may likely change or disappear in the absence of appropriate predators), and how to adjust management plans to promote evolutionary as well as ecological goals. Managers combating invasive species can be on the lookout for evolutionary changes in both invaders and native species.

Research on evolutionary mechanisms and effects should be incorporated into research programs in

applied ecology and resource management. Museum collections can be used to characterize and quantify microevolution in species of interest (Pergams and Ashley, 1999). Conservation geneticists should measure quantitative genetic variation directly rather than relying on neutral molecular variation to assess a population's short-term evolutionary potential (Reed and Frankham, 2001). Climate change biologists could employ quantitative genetics to assess genetic variability of traits subject to selection under anticipated conditions (Davis and Shaw, 2001). While demanding, these types of research efforts are the only way to assess the extent to which populations and traits may respond to altered environments. Resource management training programs should include coursework on evolutionary ecology and the concepts of evolutionarily enlightened management.

Computer-assisted PVA models such as VORTEX (Lacy, 1993) could incorporate selection coefficients when appropriate and explore adaptive responses of populations. Many of the traits documented to evolve rapidly are used as input in PVA models, including reproductive and life history traits such as offspring weight (Stearns, 1983), time to hatch and time to emerge (Hendry et al., 1998; Kinnison et al., 1998b), growth rate (Kinnison et al., 1998c), egg weight (Kinnison et al., 1998b; Stockwell and Weeks, 1999), and average age (Stearns, 1983; Reznick et al., 1997). Evolutionary responses in behavioral traits such as migratory timing (Quinn and Adams, 1996) and schooling tendency (Magurran et al., 1995) could also be modeled. Directional selection in such traits could be expressed through the incorporation of selection coefficients into PVA simulations. Selection differential S , response R , and phenotypic standard of deviation of the population before selection σ_p (Smith, 1989, p. 103) are sometimes already calculated, or are usually readily calculable from data in published microevolutionary studies. It remains to tie these changes to the progression of time and probabilistic iterations of a PVA simulation.

Attention should be given to the advantages, disadvantages and current stages of development of different conceptual approaches to evolution. How can genetical and historical approaches better accommodate the needs of managers? What other approaches might be usefully applied to conservation? One conceptual tool that deserves serious consideration when selective forces are both identified and few in number is evolutionary game theory and the ESS-concept (Evolutionarily Stable Strategies). Game theory lends itself to considering all species including the likely behavioral responses of humans in a common framework (Brown and Parman, 1994). Game theory models begin with the ecological scenario and so can easily begin with a manager's model or perspective on the conservation issue. For instance, Law and Grey (1989) propose the concept of the Evolutionarily Stable Optimal Harvest Strategy

as a means of harvesting evolving resources (e.g. fisheries) in a manner that preserves both the stock and its desirable heritable characteristics (such as size).

As a final point, incorporation of evolutionary thinking into conservation biology raises a possible philosophical contradiction between what it is we ideally hope to conserve and pragmatically what we can actually accomplish. The conservationist ideal of returning species and ecosystems to pristine and pre-disturbance conditions is often unrealistic. Rapid evolution is clearly undesirable when refuge or captive populations are maintained for reintroduction, augmentation, or as a hedge against extinction of native populations. Native environments will differ radically from captive or refuge conditions, and the process of genetic drift and selection to captive conditions will lead to populations that are no longer adapted to their native environment (Frankham and Loebel, 1992; Stockwell and Weeks, 1999). Evolutionarily enlightened management can make predictions regarding the outcomes of supportive breeding (Lynch and O'Hely, 2001; Ford, 2002) and aid in the design of captive breeding (Allendorf, 1993) and ex situ conservation programs (Hamilton, 1994) that minimize genetic losses and adaptive shifts. In other situations, rapid evolution might not always be viewed as detrimental. Is it better to lose a species to extinction altogether, or to retain a species that has been exposed for several generations to selective forces associated with human activity and has responded with evolutionary changes in traits that will assure its survival? Is it more desirable to restore an ecosystem to an independently functioning but altered state, or to a pre-disturbance state requiring continual human intervention (Brown, 1994)? Difficult as these questions may be, they can only be addressed within a framework that includes evolutionary thinking.

Acknowledgements

J. Ewel, K.C. Ewel, R. Lacy, T.P. Quinn, T.C. Shirley, J. Verner, C.J. Whelan, M.W. Schwartz and an anonymous reviewer provided constructive comments on the manuscript. We are very grateful for their efforts, even though we could not accommodate all of their divergent suggestions. O.R.W.P. was funded by a US EPA STAR Fellowship. This work was conducted in part while M.V.A. was a Sabbatical Fellow at the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation, the University of California, and the Santa Barbara Campus.

References

Able, K.P., Belthoff, J.R., 1998. Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. Proceedings of the Royal Society of London Series B—Biological Sciences 265, 2063–2071.

Abrams, P.A., 1996. Evolution and the consequences of species introductions and deletions. Ecology 77, 1321–1328.

Adams, P.B., 1980. Life history patterns in marine fishes and their consequence for fisheries management. Fishery Bulletin 78, 1–12.

Allendorf, F.W., 1993. Delay of adaptation to captive breeding by equalizing family size. Conservation Biology 7, 416–419.

Allendorf, F.W., Ryman, N., Utter, F.M., 1987. Genetics and fishery management: past present and future. In: Ryman, N., Utter, F. (Eds.), Population Genetics and Fishery Management. Washington Sea Grant Program, Seattle, WA, pp. 1–19.

Antonovics, J., Bradshaw, A.D., 1970. Evolution in closely adjacent plant populations. VII. Clinal patterns of a mine boundary. Heredity 25, 349–362.

Badyaev, A.V., Hill, G.E., Stoehr, A.M., Nolan, P.M., McGraw, K.J., 2000. The evolution of sexual size dimorphism in the house finch. II. Population divergence in relation to local selection. Evolution 54, 2134–2144.

Beissinger, S.R., Westphal, M.L., 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62, 821–841.

Benkman, C.W., 1995. The impact of tree squirrels (*Tamiasciurus*) on limber pine seed dispersal adaptations. Evolution 49, 585–592.

Berejikian, B.A., Matthews, S.B., Quinn, T.P., 1996. Effects of hatchery and wild ancestry and rearing environments on the development of agonistic behavior in steelhead trout (*Oncorhynchus mykiss*) fry. Canadian Journal of Fisheries and Aquatic Sciences 53, 2004–2014.

Berry, R.J., 1964. The evolution of an island population of the house mouse. Evolution 18, 468–483.

Berry, R.J., 1986. Genetics of insular populations of mammals, with particular reference to differentiation and founder effects in British small mammals. Biological Journal of the Linnean Society 28, 205–230.

Berry, R.J., Jakobson, M.E., Peters, J., 1978. The house mice of the Faroe islands: a study in microdifferentiation. Journal of the Zoological Society of London 185, 73–92.

Berthold, P., Helbig, A.J., Mohr, G., Querner, U., 1992. Rapid microevolution of migratory behaviour in a wild bird species. Nature 360, 668–670.

Blossey, B., Nötzold, R., 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. Journal of Ecology 83, 887–889.

Boag, P.T., Grant, P.R., 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galapagos. Science 214, 82–85.

Bone, E., Farres, A., 2001. Trends and rates of microevolution in plants. Genetica 112–113, 165–182.

Browman, H.I., 2000. 'Evolution' of fisheries science. Marine Ecology—Progress Series 208, 299–313.

Brown, C.R., Brown, M.B., 1998. Intense natural selection on body size and wing and tail asymmetry in cliff swallows during severe weather. Evolution 52, 1461–1475.

Brown, J.S., 1994. Restoration ecology: living with the prime directive. In: Bowles, M.L., Whelan, C.J. (Eds.), Restoration of Endangered Species. Cambridge University Press, Cambridge, pp. 355–380.

Brown, J.S., Parman, A.O., 1994. Consequences of size-selective harvesting as an evolutionary game. Lecture Notes in Biomathematics 99, 248–261.

Brown, J.S., Pavlovic, N.B., 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. Evolutionary Ecology 6, 360–382.

Burris, O.E., McKnight, D.E., 1973. Game transplants in Alaska. Alaska Department of Fish and Game, Game Technical Bulletin 4, 1–58.

Byrne, K., Nichols, R.A., 1999. *Culex pipiens* in London underground tunnels: differentiation between surface and subterranean populations. Heredity 82, 7–15.

Carroll, S.P., Boyd, C., 1992. Host race radiation in the soapberry bug: natural history, with the history. Evolution 46, 1052–1069.

- Carroll, S.P., Dingle, H., Klassen, S.P., 1997. Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution* 51, 1182–1188.
- Cody, M.L., Overton, J.M., 1996. Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology* 84, 53–61.
- Daehler, C.C., Strong, D.R., 1997. Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia* 110, 99–108.
- Davies, M.S., Snaydon, R.W., 1976. Rapid population differentiation in a mosaic environment. III. Measures of selection pressures. *Heredity* 36, 59–66.
- Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive response to quaternary climate change. *Science* 292, 673–679.
- Davison, A.W., Reiling, K., 1995. A rapid change in ozone resistance of *Plantago major* after summers with high ozone concentrations. *New Phytologist* 131, 337–344.
- Dobzhansky, T., 1941. *Genetics and the Origin of Species*, second ed. Columbia University Press, NY.
- Ellner, S.P., Fieberg, J., Ludwig, D., Wilcox, D., 2002. Precision of population viability analysis. *Conservation Biology* 16, 258–261.
- Faith, D.P., 1996. Conservation priorities and phylogenetic pattern. *Conservation Biology* 10, 1286–1289.
- Fiebert, J., Ellner, S.P., 2000. When is it meaningful to estimate an extinction probability? *Ecology* 81, 2040–2047.
- Fleming, I.A., Gross, M.R., 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* 43, 141–157.
- Fleming, I.A., Gross, M.R., 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* 48, 637–657.
- Foote, C.J., 1988. Male mate choice dependent on male size in salmon. *Behaviour* 100, 63–80.
- Ford, M.J., 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. *Conservation Biology* 16, 815–825.
- Frankham, R., 1995. Conservation genetics. *Annual Review of Genetics* 29, 305–327.
- Frankham, R., Loebel, D.A., 1992. Modeling problems in conservation genetics using captive *Drosophila* populations: rapid genetic adaptations to captivity. *Zoo Biology* 11, 333–342.
- Geber, M.A., Dawson, T.E., 1993. Evolutionary responses of plants to global change. In: Kareiva, P.M., Kinsolver, J.G., Huey, R.B. (Eds.), *Biotic Interactions and Global Change*. Sinauer, Sunderland MA, pp. 179–197.
- Gibbs, H.L., Grant, P.R., 1987. Oscillating selection on Darwin's finches. *Nature* 327, 511–513.
- Gilchrist, G.W., Huey, R.B., Serra, L., 2001. Rapid evolution of wing size clines in *Drosophila subobscura*. *Genetica* 112–113, 273–286.
- Gingerich, P.D., 1993. Quantification and comparison of evolutionary rates. *American Journal of Science* 293A, 453–478.
- Grant, P.R., Grant, B.R., 1995. Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* 49, 241–251.
- Groman, J.D., Pellmyr, O., 2000. Rapid evolution and specialization following host colonization in a yucca moth. *Journal of Evolutionary Biology* 13, 223–236.
- Hamilton, M.B., 1994. Ex situ conservation of wild plant species: time to reassess the genetic assumptions and implications of seed banks. *Conservation Biology* 8, 39–49.
- Haugen, T.O., Vøllestad, L.A., 2001. A century of life-history evolution in grayling. *Genetica* 112–113, 475–491.
- Healey, M.C., 1986. Optimum size and age at maturity in Pacific salmon and effects of size-selective fisheries. *Canadian Special Publication in Fisheries and Aquatic Sciences* 89, 39–52.
- Hendry, A.P., Kinnison, M.T., 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53, 1637–1653.
- Hendry, A.P., Quinn, T.P., 1997. Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. *Canadian Journal of Fisheries and Aquatic Science* 54, 75–84.
- Hendry, A.P., Hensleigh, J.E., Reisenbichler, R.R., 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon (*Oncorhynchus nerka*) within Lake Washington. *Canadian Journal of Fisheries and Aquatic Science* 55, 1387–1394.
- Hendry, A.P., Wenburg, J.K., Bentzen, P., Volk, E.C., Quinn, T.P., 2000. Rapid evolution of reproductive isolation in the wild: evidence from introduced salmon. *Science* 290, 515–518.
- Hitchings, S.P., Beebe, T.J.C., 1997. Genetic substructuring as a result of barriers to gene flow in urban *Rana temporaria* (common frog) populations: implications for biodiversity conservation. *Heredity* 79, 117–127.
- Holt, R.D., Gaines, M.S., 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology* 6, 433–447.
- Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D., Serra, L., 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287, 308–309.
- Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15, 56–61.
- Iverson, L.R., Prasad, A., Schwartz, M.W., 1999. Modeling potential future individual tree-species distributions in the eastern United States under a climate change scenario: a case study with *Pinus virginiana*. *Ecological Modeling* 115, 77–93.
- Johnson, J.I., Petersson, E., Jönsson, E., Björnsson, F.T., Järvi, T., 1996. Domestication and growth hormone alter antipredator behaviour and growth patterns in juvenile brown trout, *Salmo trutta*. *Canadian Journal of Fisheries and Aquatic Sciences* 53, 1546–1554.
- Johnston, R.F., Selander, R.K., 1964. House sparrows; rapid evolution of races in North America. *Science* 144, 548–550.
- Kettlewell, B., 1973. *The Evolution of Melanism: The Study of a Recurring Necessity*. Clarendon Press, Oxford.
- Kinnison, M.T., Hendry, A.P., 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* 112–113, 145–164.
- Kinnison, M., Unwin, M., Boustead, N., Quinn, T., 1998a. Population-specific variation in body dimensions of adult chinook salmon (*Oncorhynchus tshawytscha*) from New Zealand and their source populations, 90 years after introduction. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 554–563.
- Kinnison, M.T., Unwin, M.J., Hershberger, W.K., Quinn, T.P., 1998b. Egg size, fecundity, and development rate of two introduced New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1946–1953.
- Kinnison, M.T., Unwin, M.J., Quinn, T.P., 1998c. Growth and salinity tolerance of juvenile chinook salmon (*Oncorhynchus tshawytscha*) from two introduced New Zealand populations. *Canadian Journal of Zoology* 76, 2219–2226.
- Labelle, M., Walters, C.J., Riddell, B., 1997. Ocean survival and exploitation of coho salmon (*Oncorhynchus kisutch*) stocks from the east coast of Vancouver Island, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 1433–1449.
- Lacy, R.C., 1993. VORTEX: a computer simulation model for population viability analysis. *Wildlife Research* 20, 45–65.
- Law, R., 2000. Fishing, selection, and phenotypic evolution. *Journal of Marine Science* 57, 659–668.
- Law, R., Grey, D.R., 1989. Evolution of yields from populations with age-specific cropping. *Evolutionary Ecology* 3, 343–359.
- Lee, C.E., 1999. Rapid and repeated invasions of fresh water by the copepod *Eurytemora affinis*. *Evolution* 53, 1423–1434.
- Losos, J.B., Schoener, T.W., Warheit, K.I., Creer, D., 2001. Experimental studies of adaptive differentiation in Bahamian Anolis lizards. *Genetica* 112, 399–415.

- Ludwig, D., 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80, 298–310.
- Lynch, M., 1996. A quantitative-genetic perspective on conservation issues. In: Avise, J.C., Hamrick, J.L. (Eds.), *Conservation Genetics*. Chapman and Hall, New York, pp. 471–501.
- Lynch, M., O'Hely, M., 2001. Captive breeding and the genetic fitness of natural populations. *Conservation Genetics* 2, 363–378.
- Magurran, A.E., Seghers, B.H., Shaw, P.W., Carvalho, G.R., 1995. The behavioral diversity and evolution of guppy, *Poecilia reticulata*, populations in Trinidad. *Advances in the Study of Behavior* 24, 155–202.
- Magurran, A.E., Seghers, B.H., Carvalho, G.R., Shaw, P.W., 1992. Behavioral consequences of an artificial introduction of guppies (*Poecilia reticulata*) in Trinidad—evidence for the evolution of anti-predator behaviour in the wild. *Proceedings of the Royal Society of London, Series B* 248, 117–122.
- McCarthy, M.A., Possingham, H.P., Day, J.R., Tyre, A.J., 2001. Testing the accuracy of population viability analysis. *Conservation Biology* 1030–1038.
- Morgan, K.K., Hicks, J., Spitze, K., Latta, L., Pfrender, M.E., Weaver, C.S., Ottone, M., Lynch, M., 2001. Patterns of genetic architecture for life-history traits and molecular markers in a subdivided species. *Evolution* 55, 1753–1761.
- Nelson, K., Soule, M., 1987. Genetical conservation of exploited fishes. In: Ryman, N., Utter, F. (Eds.), *Population Genetics and Fishery Management*. Washington Sea Grant Program, Seattle, WA, pp. 345–368.
- Orians, G., 1998. Human behavioral ecology: 140 years without Darwin is too long. *Bulletin of the Ecological Society of America* 79, 15–28.
- O'Steen, S., Cullum, A.J., Bennett, A.F., 2002. Rapid evolution of escape ability in Trinidadian guppies. *Evolution* 56, 776–784.
- Palumbi, S.R., 2001. Humans as the world's greatest evolutionary force. *Science* 293, 1786–1790.
- Parnell, J., 1995. Systematics helps identify conservation priorities. *Conservation Biology* 9, 972–973.
- Patton, J.L., Yang, S.Y., Myers, P., 1975. Genetic and morphological divergence among introduced rat populations (*Rattus rattus*) of the Galapagos archipelago, Ecuador. *Systematic Zoology* 24, 296–310.
- Pergams, O.R.W., Ashley, M.V., 1999. Rapid morphological change in Channel Island deer mice. *Evolution* 53, 1573–1581.
- Pergams, O.R.W., Ashley, M.V., 2001. Microevolution in island rodents. *Genetica* 112–113, 245–256.
- Pimm, S.L., 1990. The decline of the Newfoundland crossbill. *Trends in Ecology and Evolution* 5, 350–351.
- Podolsky, R.H., 2000. Genetic variation for morphological and allozyme variation in relation to population size in *Clarkia dudleyana*, and endemic annual. *Conservation Biology* 15, 412–423.
- Quinn, T.P., Adams, D.J., 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77, 1151–1162.
- Quinn, T.P., Foote, C.J., 1994. The effects of body size and sexual dimorphism on the reproductive behaviour of sockeye salmon, *Oncorhynchus nerka*. *Animal Behaviour* 48, 751–761.
- Quinn, T.P., Kinnison, M.T., 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. *Oecologia* 121, 273–282.
- Quinn, T.P., Unwin, M.J., Kinnison, M.T., 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. *Evolution* 54, 1372–1385.
- Quinn, T.P., Kinnison, M.T., Unwin, M.J., 2001. Evolution of chinook salmon (*Oncorhynchus tshawytscha*) populations in New Zealand: pattern, rate, and process. *Genetica* 112, 493–513.
- Reed, D.H., Frankham, R., 2001. How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. *Evolution* 55, 1095–1103.
- Reisenbichler, R.R., 1997. Genetic factors contributing to declines of anadromous salmonids in the Pacific Northwest. In: Stouder, D.J., Bisson, P.A., Naiman, R.J. (Eds.), *Pacific Salmon and Their Ecosystems: Status and Future Options*. Chapman and Hall, New York, pp. 223–244.
- Reznick, D.N., Shaw, F.H., Rodd, F.H., Shaw, R.G., 1997. Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275, 1934–1937.
- Reznick, D.N., Ghalambor, C.K., 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* 112, 183–198.
- Ricker, W.E., 1981. Changes in the average size and average age of Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 38, 1636–1656.
- Rijnsdorp, A.D., 1993. Fisheries as a large-scale experiment on life-history evolution—disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96, 391–401.
- Rodriguez-Trelles, F., Rodriguez, M.A., 1998. Rapid micro-evolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evolutionary Ecology* 12, 829–838.
- Rogers, D.E., 1987. The regulation of age at maturity in Wood River sockeye salmon (*Oncorhynchus nerka*). *Canadian Special Publication in Fisheries and Aquatic Sciences* 96, 78–89.
- Schwartz, M.W., Iverson, L.R., Prasad, A.M., 2001. Predicting the potential future distribution of four tree species in Ohio, USA, using current habitat availability and climatic forcing. *Ecosystems* 4, 568–581.
- Scholz, F.H., Gregorius, R., Rudin, D. (Eds.), 1989. *Genetic Effects of Air Pollutants in Forest Tree Populations*. Springer-Verlag, Berlin.
- Sieving, K.E., Willson, M.F., 1998. Nest predation and avian species diversity in northwestern forest understory. *Ecology* 79, 2391–2402.
- Smith, M., 1989. *Evolutionary Genetics*. Oxford University Press.
- Smith, T.B., Freed, L.A., Lepson, J.K., Carothers, J.H., 1995. Evolutionary consequences of extinctions in populations of a Hawaiian honeycreeper. *Conservation Biology* 9, 107–113.
- Soltis, P.S., Gitzendanner, M.A., 1999. Molecular systematics and the conservation of rare species. *Conservation Biology* 13, 471–483.
- Stearns, S.C., 1983. The genetic basis of differences in life-history traits among six populations of mosquitofish since their introduction to Hawaii in 1905: rates of evolution, heritabilities, and developmental plasticity. *American Zoologist* 23, 65–76.
- Stockwell, C.A., Mulvey, M., 1998. Phosphogluconate dehydrogenase polymorphism and salinity in the White Sands pupfish. *Evolution* 52, 1856–1860.
- Stockwell, C.A., Weeks, S.C., 1999. Translocations and rapid evolutionary responses in recently established populations of western mosquitofish (*Gambusia affinis*). *Animal Conservation* 2, 103–110.
- Stokes, K., Law, R., 2000. Fishing as an evolutionary force. *Marine Ecology Progress Series* 208, 299–313.
- Thompson, J.N., 1998. Rapid evolution as an ecological process. *Trends in Ecology and Evolution* 13, 329–332.
- Unwin, M.J., Glova, G.J., 1997. Changes in life history parameters in a naturally spawning population of chinook salmon (*Oncorhynchus tshawytscha*) associated with releases of hatchery-reared fish. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 1235–1245.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Ward, J.K., Antonovics, J., Thomas, R.B., Strain, B.R., 2000. Is atmospheric CO₂ a selective agent on model C3 annuals? *Oecologia* 123, 330–341.
- Willson, M.F., 2002. The fallacy of the superfluous males. *Conservation Biology* 16, 557–559.
- Wu, L., Kruckeberg, A.L., 1985. Copper tolerance in two legume species from a copper mine habitat. *New Phytologist* 99, 565–570.