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Rapid Adaptation and Conservation

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Recent work has demonstrated that adaptive evolution often occurs on contemporary time scales (years to decades), making it of particular relevance to conservation planning (Ashley et al. 2003; Stockwell et al. 2003). Reports of rapid evolution span a variety of species, traits, and situations, suggesting that rapid adaptation is the norm rather than the exception (Hendry & Kinnison 1999; Kinnison & Hendry 2001; Stockwell et al. 2003). Furthermore, rapid adaptation is often associated with the same anthropogenic factors responsible for the current extinction crisis, including overharvest, habitat degradation, habitat fragmentation, and exotic species (Stockwell et al. 2003) and thus has immediate relevance to conservation biology. Here, we briefly consider the potential importance of rapid adaptation to the conservation of actively managed species and to the spread and control of exotic species.

Rapid adaptation is of particular concern for captive populations (i.e., "domestication;" Fleming & Gross 1993; Frankham 1995; Margan et al. 1998) as well as for "refuge" populations established as a hedge against extinction (Stockwell & Weeks 1999). Such actively managed populations may rapidly diverge from their parental populations to the point that they are maladapted to their ancestral habitat. Similarly, recent genetic models suggest that augmentation of native populations from captive stock ("supportive breeding") will likely reduce a wild population's fitness (Lynch & O'Hely 2001; Tufto 2001; Ford 2002). It is also possible that selection pressures may change and thus limit the success of repatriation programs. For instance, natural selection at release sites may be so strong that populations go extinct even in the process of adapting to the "new" environment (Lynch 1996). One solution would be to introduce populations to intermediate environments. Another approach may be to "select" phenotypes most likely to succeed in the new environment (Hendry et al. 2003). These observations suggest that adaptive responses should be a major consideration for actively managed species.

Rapid adaptation is also relevant to one of the most daunting problems facing conservation biologists, the spread of nonindigenous species. The problem of exotic species becomes even less tractable with the prospect that such species may be rapidly adapting to their new environments (Stockwell et al. 2003). In fact, the introduction of populations into novel environments is the most common factor associated with rapid adaptation (Reznick & Ghalambor 2001). Exotic species often persist at low numbers before becoming invasive (Schmitz et al. 1997). This pattern may reflect hybridization (Ellstrand & Schierenbeck 2000) or directional selection, in which a lag occurs as the population adapts before it can enter a population growth phase. This "lag effect" may provide the best opportunity for aggressive control, effectively placing managers in a race with adaptive evolution to establish control over exotic species.

Finally, exotic species have the potential to evolve resistance to various control measures. Over 500 arthropod species have evolved pesticide resistance (Goerghiou & Lagunes-Tejeda 1991). The control of exotic species is also likely to be an uphill battle against rapid adaptation. Therefore, control efforts should be considered in an evolutionary context. For instance, gene flow between populations at different adaptive peaks is expected to reduce population fitness (Boulding & Hay 2001). Thus, interpopulation gene flow may be a potential control method for exotic species that have diverged from their ancestral population. Another approach would be to use multiple control measures simultaneously to reduce the probability of evolved resistance to any given control measure. However, this approach may not work if resistance responses are not independent (Tabashnik et al. 1997).

We have briefly outlined a few contexts in which species' adaptive responses are relevant to conservation biology. Adaptive responses are germane to other contexts such as overharvesting of populations (Conover 2000; Conover & Munch 2002). Why has the integration of rapid adaptation into conservation biology been relatively limited? First, the thinking that species are fixed entities that only evolve over geological time is customary in fields ranging from the biology of global change to

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population viability analysis (Ashley et al. 2003). Second, conservation genetics research has been dominated by the use of molecular markers that are presumed neutral. While such markers may provide useful information about historical gene flow patterns and evolutionary lineages, they are not a good substitute for directly considering important quantitative traits that may be responding to changing environments (Lynch 1996; Bekessy et al. 2002). Finally, measuring selective forces and predicting evolutionary change is challenging and requires a substantial investment of resources, a retooling of established research programs, and new training (and retraining) in evolutionary ecology. Despite these obstacles, we submit that conservation biology will become a more effective endeavor if adaptive responses of organisms are more consistently considered and creatively investigated.

The incorporation of adaptive evolution into conservation plans can be pursued in both the short and long term. In the short term, conservation and evolutionary biologists should collaborate to develop conservation plans that directly address evolutionary concerns. Perhaps it is time for a second joint meeting of the Society for Conservation Biology and the Society for the Study of Evolution. In the long term, a re-evaluation of conservation biology curricula may be in order. At the minimum, evolution should be a required course for all students majoring in conservation biology. Such evolution courses should cover adaptive evolution of quantitative traits and the activities of humans as potent evolutionary forces that drastically alter selection regimes. As more resources become available, additional graduate-level courses can be developed in the interdisciplinary area of evolutionary conservation, which will lead to evolutionarily enlightened management.

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Literature Cited

Ashley, M. V., M. F. Willson, O. R. W. Pergrams, D. J. O'Dowd, S. M. Gende, and J. S. Brown. 2003. Evolutionary enlightened management. Biological Conservation 111:115–123.

- Bekessy, S. A., R. A. Ennos, M. A. Burgman, A. C. Newton, and P. K. Ades. 2002. Neutral DNA markers fail to detect genetic divergence in an ecologically important trait. Biological Conservation 110:267-275.
- Boulding, E. G., and T. Hay. 2001. Genetic and demographic parameters determining population persistence. Heredity **86**:313–324.
- Conover, D. 2000. Darwinian fishery science. Marine Ecology Progress Series **208**:299–313.
- Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297:94–96.
- Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proceedings of the National Academy of Sciences, U.S.A. **97**:7043–7050.
- Fleming, I. R., and M. R. Gross. 1993. Breeding success of hatchery and wild coho salmon (*Oncorbynchus kisutch*) in competition. Ecological Applications 3:230–245.
- 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.
- Goerghiou, G. P., and A. Lagunes-Tejeda. 1991. The occurrence of resistance to pesticides in arthropods. Food and Agriculture Organization, Rome.
- Hendry, A. P., and M. T. Kinnison. 1999. The pace of modern life: measuring rates of contemporary microevolution. Evolution 53:1637–1653.
- Hendry, A. P., B. H. Letcher, and G. Gries. 2003. Estimating natural selection acting on stream-dwelling Atlantic salmon: implications for the restoration of extirpated populations. Conservation Biology 17:795-805.
- Kinnison, M. T., and A. P. Hendry. 2001. The pace of modern life. II. From rates of contemporary microevolution to pattern and process. Genetica 112-113:145-164.
- Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pages 471-501 in J. C. Avise and J. L. Hamrick, editors. Conservation genetics: case studies from nature. Chapman & Hall, New York.
- Lynch, M., and M. O'Hely. 2001. Captive breeding and the genetic fitness of natural populations. Conservation Genetics 2:363–378.
- Margan, S. H., R. K. Nurthen, M. E. Montgomery, L. M. Woodworth, E. H. Lowe, D. A. Briscoe, and R. Frankham. 1998. Single large or several small? Population fragmentation in the captive management of endangered species. Zoo Biology 17:467-480.
- Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. Genetica 112-113:183-198.
- Schmitz, D. C., D. Simberloff, R. H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impact of nonindigenous plants. Pages 39-61 in D. Simberloff, D. C. Schmitz, and T. C. Brown, editors. Strangers in paradise. Island Press, Washington, D.C.
- Stockwell, C. A., A. P. Hendry, and M. T. Kinnison. 2003. Contemporary evolution meets conservation biology. Trends in Ecology & Evolution 18:94-101.
- Stockwell, C. A., and S. C. Weeks. 1999. Translocations and rapid evolutionary responses in recently established populations of western mosquitofish (*Gambusia affinis*). Animal Conservation 2:103–110.
- Tabashnik, B. E., Y.-B. Liu, N. Finson, L. Masson, and D. G. Heckel. 1997. One gene in diamondback moth confers resistance to four *Bacillus thuringiensis* toxins. Proceedings of the National Academy of Sciences of the United States of America 94:1640-1644.
- Tufto, J. 2001. Effects of releasing maladapted individuals: a demographic-evolutionary model. The American Naturalist 158: 331-340.