



2-19-2002

Ecological genetics and the translocation of native fishes: emerging experimental approaches

Craig A. Stockwell

North Dakota State University, Fargo, North Dakota

Paul L. Leberg

University of Louisiana, Lafayette

Follow this and additional works at: <https://scholarsarchive.byu.edu/wnan>

Recommended Citation

Stockwell, Craig A. and Leberg, Paul L. (2002) "Ecological genetics and the translocation of native fishes: emerging experimental approaches," *Western North American Naturalist*. Vol. 62 : No. 1 , Article 4. Available at: <https://scholarsarchive.byu.edu/wnan/vol62/iss1/4>

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

ECOLOGICAL GENETICS AND THE TRANSLOCATION OF NATIVE FISHES: EMERGING EXPERIMENTAL APPROACHES

Craig A. Stockwell¹ and Paul L. Leberg²

ABSTRACT.—Conservation biologists often use translocations to augment small populations, establish “refuge” populations, or reestablish populations into historic habitat. For reasons that are poorly understood, translocations often fail. Further, translocations have both short- and long-term consequences for the evolutionary ecology of the targeted taxa. Unfortunately, most information on translocations has been derived from descriptive studies. Recent experimental approaches have provided new data to address a variety of topics associated with translocations, including inbreeding, outbreeding, the relationship between heterozygosity and fitness, and rapid evolution in populations established by translocation. We focus on genetic and ecological aspects of translocations but recognize that contributions from other fields will be essential for the long-term success of many translocation programs. Ongoing research regarding host-parasite interactions points out the need for extensive ecological data as well as genetic data to make informed decisions regarding translocations. Hypotheses derived from this field are ripe for rigorous experimental examination.

Key words: rapid evolution, adaptive management, reintroduction, inbreeding, outbreeding, local adaptation, genetic bottleneck.

Translocating animals has become a widely used tool in the conservation of rare and endangered species (Williams et al. 1988, Griffith et al. 1989); this is especially true for desert fishes (Hendrickson and Brooks 1991, Minckley 1995). Historically, translocations were often conducted in an emergency context to save a rare species from extinction (Miller and Pister 1971, Minckley et al. 1991, Minckley 1995). However, translocations are now used in a more deliberate manner. Typically, they occur in 4 contexts: to mitigate effects of proposed economic development, to augment established populations, to create refuge populations, and to reestablish historic populations. Following Wolf et al. (1996), we consider translocations to include the intentional release of either wild caught or captive reared individuals.

Translocations will probably continue to occur in the management of rare species. More than 80% of recovery plans for endangered and threatened fishes call for some form of translocation (Williams et al. 1988). However, translocation programs typically have low success rates, and factors associated with translocation failure are poorly understood (Hendrickson and Brooks 1991).

Our objective is to discuss recent research approaches that should prove useful in understanding factors affecting success of translocation. Experimental manipulations of populations together with new analytical techniques can provide important insights into how genetic and ecological processes affect translocation success. We focus on small fishes because they can be experimentally manipulated more easily than other vertebrates and because numerous fish species have been the subject of past translocations (Hendrickson and Brooks 1991, Fuller et al. 1999). The results of both manipulative and management translocation experiments involving fish populations will have management implications for not only this important group but also many other vertebrate taxa.

Traditional translocation research has emphasized genetics (Turner 1984, Vrijenhoek et al. 1985, Allendorf and Ryman 1987, Quattro and Vrijenhoek 1989, Echelle 1991, Leberg 1991, Ellsworth et al. 1994, Leberg et al. 1994, Hedrick 1995, Stockwell et al. 1996, Leberg and Ellsworth 1999), but these data are best interpreted in an ecological context. Most translocation research has been descriptive; however, recent studies have applied experimental

¹Department of Zoology, Stevens Hall, North Dakota State University, Fargo, ND 58105.

²Department of Biology, University of Louisiana, Lafayette, LA 70504.

approaches to address a variety of translocation topics, including effects of inbreeding (Leberg 1990a), outbreeding (Philipp 1991, Leberg 1993), relationship between heterozygosity and fitness (Quattro and Vrijenhoek 1989, Sheffer et al. 1997), and evolution in recently established populations (Reznick et al. 1990, Stockwell and Mulvey 1998, Stockwell and Weeks 1999).

EXPERIMENTAL ASSESSMENTS OF CONSEQUENCES OF GENETIC VARIATION

Populations established by translocation often exhibit reduced genetic variability (Allendorf and Ryman 1987, Leberg 1992, Stockwell et al. 1996, but see Turner 1984). Leberg (1990a) established experimental populations of eastern mosquitofish (*Gambusia holbrooki*) that differed in levels of genetic variation. Populations founded by small numbers of individuals had reduced genetic variation and lower population growth rates (Leberg 1990a). This work supported the basis for suggestions that a minimum number of individuals be used to found new populations (Allendorf and Ryman 1987). However, even when numerous individuals are translocated, bottlenecks may occur early in population establishment, leading to reduced genetic diversity (Stockwell et al. 1996). Such effects occur in an ecological context; reductions in population size and consequent reductions in genetic diversity may be due to novel ecological conditions.

Gene flow from parental populations to refuge populations is one solution to minimize loss of genetic variability in refuge populations (Stockwell et al. 1996). Further, populations established by translocation should be periodically surveyed for genetic diversity (Allendorf and Ryman 1987, Stockwell et al. 1996). To detect changes in genetic diversity, large numbers of polymorphic loci and alleles should be used (Leberg 1992, Richards and Leberg 1996); thus, highly polymorphic microsatellite loci may prove useful as a monitoring tool. For instance, by using microsatellites, Parker et al. (1999) detected genetic structure in the Gila topminnow (*Poeciliopsis occidentalis occidentalis*) that was not observed with either allozymes or mtDNA. Spencer et al. (2000) found levels of microsatellite variation to be highly correlated to founder number in experimental populations of *Gambusia affinis*.

Genetic variability has been considered an important criterion in selecting stock for reintroduction efforts with the Gila topminnow (Vrijenhoek et al. 1985, Quattro and Vrijenhoek 1989, Quattro et al. 1996). Quattro and Vrijenhoek (1989) raised fish from 3 populations of the Gila topminnow under common-garden conditions to assess fitness-related characters. They found that the stock with the highest heterozygosity (Sharp Spring) had higher survival, higher fecundity, and higher developmental stability as measured by fluctuating asymmetry (FA) than did the less heterozygous Monkey Spring population (Quattro and Vrijenhoek 1989). Recently, Sheffer et al. (1997) repeated this experiment and found no difference in stock performance. This discordance may reflect differences in laboratory conditions. For instance, 12-week survivorship was substantially lower in the first study (45–56%) than in the latter study (93–96%). The difference in survivorship suggests that the first study included relatively stressful environmental conditions compared to the second study. Thus, it is possible that stock differences may appear only during suboptimal conditions. This suggests a need for additional ecological work to assess the interaction between environmental conditions and genetic background on fitness.

One means to increase genetic variability would be to proliferate outcrossing among populations, thereby increasing genetic diversity and possibly stock performance (Vrijenhoek et al. 1985, Meffe and Vrijenhoek 1988, Hedrick 1995). Leberg (1993) experimentally examined outcrossing effects by crossing populations of eastern mosquitofish from the same river drainage. For a pair of populations separated by 10 km, and with similar allele frequencies, there were no positive or detrimental effects on the growth of outcrossed populations. Population growth rates were lower for outcrossed groups than for pure stocks when the 2 parental stocks were separated by 100 km and had statistically significant differences in allele frequencies. This outbreeding depression of growth rates may affect population viability of small or recently established populations (Leberg 1993). Philipp (1991) also conducted experimental work to examine the role of outbreeding between subspecies of largemouth bass (*Micropterus salmoides*). This experiment also suggested outbreeding

depression, which was interpreted as a disruption of locally adapted gene-complexes (Philipp 1991). Future research should consider the relationship between genetic differentiation and outbreeding depression. This information is especially relevant to the design of translocation programs.

Locally adapted gene complexes are of particular interest because they illustrate the interplay between local selective regime and genetic architecture. Local adaptation is likely to involve quantitative traits such as behavior, morphology, or life history characters, but our knowledge of how translocations may influence quantitative traits has received little attention. Further, such traits are subject to natural selection (Lynch 1996) and may evolve in response to novel environmental conditions in refuge habitats (see Stockwell and Weeks 1999).

The issue of locally adapted gene-complexes is also pertinent for remnant populations of species formerly occurring over large spatial scales. For instance, genetic surveys of the razorback sucker (*Xyrauchen texanus*) suggest a lack of genetic structure, and yet concern regarding potential outcrossing effects has stalled efforts to reintroduce fish into their former range (Dowling et al. 1996). This concern may be valid. Lack of genetic structure for neutral markers does not necessarily represent a lack of local adaptation at structural or regulatory loci (Allendorf 1983). More experimental research is needed to assess the effects of outbreeding depression resulting from mixing populations with different levels of genetic differentiation and geographic isolation. Such information will aid in the assessment of management risks associated with outcrossing.

RAPID EVOLUTION IN TRANSLOCATED POPULATIONS

Another evolutionary consequence of translocations involves rapid phenotypic shifts in introduced populations. Stockwell and Weeks (1999) reported rapid life history evolution in recently established populations of western mosquitofish (*Gambusia affinis*). A common-garden experiment confirmed a genetic basis for 2 life history traits shown to vary among 4 populations derived from the same population in the late 1930s (Stockwell and Weeks 1999, Stockwell and Vinyard 2000). Thus, these

recently established populations had undergone rapid evolutionary divergence. A recent analysis suggested this case of evolution may have occurred over a 4-year period (12–16 generations; Stockwell and Vinyard 2000).

A variety of other studies have documented rapid evolution for fishes introduced to new localities (Stearns 1983, Reznick et al. 1990, Hendry et al. 1998, Kinnison et al. 1998, Stockwell and Mulvey 1998); however, identifying the selective factor(s) associated with such evolution can be difficult. For example, Reznick et al. (1990) originally assumed that size-selective predation was responsible for rapid life history evolution in a population of Trinidadian guppies introduced to a site with novel predation pressure. However, new data on this system suggest that although predation probably plays a primary role, the specific mechanism remains uncertain (Reznick et al. 1996). This demonstrates the difficulty of predicting how translocated populations may respond to novel ecological conditions, even in well-studied systems.

Rapid evolution is of particular concern when target populations have been established as “genetic replicates” for an endangered species (Stockwell and Weeks 1999). For instance, concern for the Devil’s Hole pupfish (*Cyprinodon diabolis*) led to establishment of refuge populations to provide stock for reintroduction if the native population was extirpated (Williams 1977). Pupfish from one refuge site differed morphologically from Devil’s Hole pupfish (Williams 1977). Unfortunately, extirpation of this refuge population precluded assessment of whether the change was due to developmental plasticity or rapid evolution.

Rapid evolutionary divergence is most likely when refuge habitats are not well matched to the ecology of the native habitat. Even under “best case” scenarios, one or more ecological factors are likely to differ between the native site and the refuge site, which could potentially lead to rapid evolution in the refuge site. Ultimately, rapid evolutionary divergence may result in refuge populations that are maladapted to their original native habitat. One solution may be to provide artificial gene flow between native and refuge populations to retard evolutionary shifts in the refuge population. However, such a strategy could render the refuge population less viable. Additional data

are necessary to assess how managed migration rates may influence population divergence.

TRANSLOCATIONS AND PARASITE EXPOSURE HISTORY

Translocations may alter important ecological relationships for target taxa. For instance, translocations can alter the relationship between rare species and parasites in 4 ways. First, parasites novel to the introduction site may be introduced along with the targeted taxon (Hoffman and Schubert 1984). Second, translocated populations may encounter parasites that did not occur in the native habitat (Sakanari and Moser 1990). Third, introduced populations may escape historic parasites as a result of conditions unfavorable to the parasite in the refuge habitat. Finally, inadequate sampling may result in loss of parasites during translocation. Parasites are typically over-dispersed; thus, if the founding population is small, the entire parasite community is unlikely to be established.

These problems are especially likely for species occupying a diversity of habitat types. For example, rainbow trout (*Oncorhynchus mykiss*) populations vary in resistance to the myxosporidean *Ceratomyxa shasta*, presumably as a result of their history of exposure to this parasite (Bartholomew et al. 1992). Resistance to this parasite has a genetic basis, and hybrids between resistant and nonresistant strains show intermediate resistance (Ibarra et al. 1992). This has proven important in one situation where introgression has occurred between non-resistant hatchery stock and a resistant native population (Currens et al. 1997).

Recent work on the White Sands pupfish (*Cyprinodon tularosa*) demonstrates how translocations may alter historic host-parasite associations. This state-listed threatened species occupies 4 isolated localities in southern New Mexico: Malpais Spring, Salt Creek, Mound Spring, and Lost River. The latter 2 populations were derived by translocation from the Salt Creek population in the 1970s (Stockwell et al. 1998). These historic translocations resulted in altered parasite communities for the introduced populations (Stockwell and Collyer unpublished data). Altered parasite communities are of most importance if parasitism is shown to be costly. Recent experimental work has shown that parasitism has both lethal and

sublethal effects on White Sands pupfish (Collyer 2000). Future work in this system will focus on the genetics of host response to parasitism.

In other systems genetics play a role in the physiological responsiveness of individuals to parasites. For example, experiments have shown genetic variation for resistance to the parasite *Gyrodactylus* in topminnows (*Poeciliopsis*) and guppies (*Poecilia reticulata*; Madhavi and Anderson 1985, Leberg and Vrijenhoek 1994). There is only limited knowledge of the genetic basis for differences in parasite susceptibility, but candidate loci include the major histocompatibility complex (MHC). Hedrick and Parker (1998) have found substantial MHC variation among populations of the endangered Gila topminnow. If this variation is associated with genotypic differences in response to parasite infection, then genetic surveys of source stocks might allow managers to design translocation programs to restore populations in the face of threats from pathogens.

These examples demonstrate how a broad research perspective is necessary to develop successful translocation programs for endangered species. We believe that many advances will be made as interdisciplinary approaches are applied. For example, many of the genetic studies we have discussed involve assessment of phenotypic and genetic responses of populations to novel ecological conditions in the new habitat.

TRANSLOCATIONS AS MANAGEMENT EXPERIMENTS

The experimental nonessential clause in the Endangered Species Act (section 10j) allows for the experimental establishment of populations. This ruling has been used extensively to establish populations under politically adverse conditions (Hendrickson and Brooks 1991). However, in our opinion the vast majority of such stockings do not qualify as "experimental" in a scientific sense, and we are unaware of any efforts to conduct replicated experimental translocations with rare taxa. This is unfortunate because much can be learned when populations are transferred to new environments (sensu Reznick et al. 1990, 1996, Stockwell and Weeks 1999).

One potential approach is to establish populations in artificial habitats where experimental

control can be achieved. This would allow managers to create refuge populations for endangered species while addressing critical questions relevant to translocation biology. We recognize that complete replication of native ecological conditions will not be achieved, but such an approach allows more experimental control. Further, this approach has an additional benefit of avoiding conflicts with taxa native to refuge sites.

In addition to the formal experiments discussed above, translocations can be viewed as management experiments (Leberg 1990b). Translocations provide unique opportunities to further explore ecological requirements of targeted taxa. Application of information resulting from management activities such as translocations is the *essence* of adaptive management (Holling 1978, Walters 1986). Prior to the release of individuals, tissue samples should be collected from translocated individuals, as well as from members of the species already present at the release site. For researchers to fully benefit from experiences, translocation attempts should be carefully documented (Minckley 1995). In many cases monitoring has not been undertaken following the translocation of fish (Hendrickson and Brooks 1991). When monitoring is included, techniques and definitions of success vary widely (Hendrickson and Brooks 1991), and efforts often go unrecorded in the peer-reviewed literature (Minckley 1995). These problems make it difficult to assess broad patterns associated with translocation failure (Hendrickson and Brooks 1991, Minckley 1995). Others have pleaded for better documentation of translocations (Hendrickson and Brooks 1991, Minckley 1995), but data on translocations would be more useful if archived in a central database; for a similar database see Fuller et al. (1999). Therefore, we recommend the creation of a web-site database for archiving translocation data in a standardized format. Others have assessed factors associated with translocation success by analysis of data obtained from resource agencies (Griffith et al. 1989, Wolf et al. 1996). A centralized database would facilitate such analyses and help to standardize monitoring efforts and definitions of translocation success.

Translocation is a common tool in the conservation of rare species, and yet many questions remain as to the long-term effects of this strategy. Much of the recent experimental

research has focused on "model systems," but we suggest that similar experimental approaches be used with target taxa. It is striking that despite the widespread use of translocations, very few translocations have been conducted in an experimental context (but see Vrijenhoek 1989). The experimental opportunities associated with translocated populations are an untapped resource.

ACKNOWLEDGMENTS

We appreciate discussions with M. Collyer, T. Crowl, P. Fuller, K. Miller, M. Mulvey, R. Sheffer, S. Swift, J. Williams, and an anonymous reviewer. CAS was supported by Department of Defense Legacy Grant #DAC A87-00-H-0014 administered by M.H. Reiser, 49 CES/CEV Environmental Flight, Holloman Air Force Base. CAS would like to dedicate this manuscript to the memory of Dr. Gary L. Vinyard, teacher, mentor, and good friend.

LITERATURE CITED

- ALLENDORE, F.W. 1983. Isolation, gene flow, and genetic differentiation among populations. Pages 51–65 in C. Schonewald-Cox, S. Chambers, B. MacBryde, and L. Thomas, editors, *Genetics and conservation*. Benjamin/Cummings, Menlo Park, CA.
- ALLENDORE, F.W., AND N. RYMAN. 1987. Genetic management of hatchery stocks. Pages 141–159 in N. Ryman and F. Utter, editors, *Population genetics and fishery management*. Washington Sea Grant, Seattle, WA.
- BARTHOLOMEW, J.L., J.S. ROHOVEC, AND J.L. FRYER. 1992. *Ceratomyxa shasta* infections of salmonid fish. Proceedings of the OJI international symposium on salmonid disease. Hokkaido University Press, Sopor, Japan.
- COLLYER, M.L. 2000. The costs of parasitism for White Sands pupfish (*Cyprinodon tularosa*) infected by white grubs (Diplostomatidae). Master's thesis, North Dakota State University, Fargo.
- CURRENS, K.P., A.R. HEMMINGSEN, R.A. FRENCH, D.A. BUCHANAN, C.B. SCHRECK, AND H.W. LI. 1997. Introgression and susceptibility to disease in a wild population of rainbow trout. *North American Journal of Fisheries Management* 17:1065–1078.
- DOWLING, T.E., W.L. MINCKLEY, AND P.C. MARSH. 1996. Mitochondrial DNA diversity within and among populations of razorback sucker (*Xyrauchen texanus*) as determined by restriction endonuclease analysis. *Copeia* 1996:542–550.
- ECHELLE, A.A. 1991. Conservation genetics and genetic diversity in freshwater fishes of western North America. Pages 141–153 in W.L. Minckley and J.E. Deacon, editors, *Battle against extinction*, University of Arizona Press, Tucson.
- ELLSWORTH, D.L., R.L. HONEYCUTT, N.J. SILVY, M.H. SMITH, J.W. BICKHAM, AND W.K. KLIMSTRA. 1994.

- White-tailed deer restoration to the southeastern United States: evaluating genetic variation. *Journal of Wildlife Management* 58:686–697.
- FULLER, P.L., L.G. NICO, AND J.D. WILLIAMS. 1999. Non-indigenous fishes introduced into inland waters of the United States. American Fisheries Society.
- GRIFFITH, B.J., M. SCOTT, J.W. CARPENTER, AND C. REED. 1989. Translocation as a species conservation tool: status and strategy. *Science* 245:477–480.
- HEDRICK, P.W. 1995. Gene flow and genetic restoration: the Florida panther as a case study. *Conservation Biology* 9:996–1007.
- HEDRICK, P.W., AND K.M. PARKER. 1998. MHC evolution in the endangered Gila topminnow. *Evolution* 52: 194–199.
- HENDRICKSON, D.A., AND J.E. BROOKS. 1991. Transplanting short-lived fishes in North American deserts: review, assessment and recommendations. Pages 283–293 in W.L. Minckley and J.E. Deacon, editors, *Battle against extinction*. University of Arizona Press, Tucson.
- HENDRY, A.P., J.E. HENSLEIGH, AND R.R. REISENBICHLER. 1998. Incubation temperature, developmental biology, and the divergence of sockeye salmon within Lake Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1387–1394.
- HOFFMAN, G.L., AND G. SCHUBERT. 1984. Some parasites of exotic fishes. Pages 233–266 in W.R. Courtney, Jr., and J.R. Stauffer, Jr., editors, *Distribution, biology, and management of exotic fishes*. Johns Hopkins University Press, Baltimore, MD.
- HOLLING, C.S. 1978. *Adaptive environmental assessment and management*. John Wiley and Sons, New York.
- IBARRA, A.M., R.P. HEDRICK, AND G.A.E. GALL. 1992. Inheritance of susceptibility to *Ceratomyxa shasta* (Myxozoa) in rainbow trout and the effect of length of exposure on the liability to develop ceratomyxosis. *Aquaculture* 104:217–229.
- KINNISON, M.T., M.J. UNWIN, W.K. HERSHBERGER, AND T.P. QUINN. 1998. Egg size, fecundity and developmental rate of two introduced New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1946–1953.
- LEBERG, P.L. 1990a. Influence of genetic variability on population growth: implications for conservation. *Journal of Fish Biology* 37(supplement A):193–195.
- _____. 1990b. Genetic considerations in the design of introduction programs. *Transactions of the North American Wildlife and Natural Resources Conference* 55:609–619.
- _____. 1991. Effects of bottlenecks on genetic divergence in populations of the wild turkey. *Conservation Biology* 5:522–530.
- _____. 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution* 46:477–494.
- _____. 1993. Strategies for population reintroduction: effects of genetic variability on population growth and size. *Conservation Biology* 7:194–199.
- LEBERG, P.L., AND D.L. ELLSWORTH. 1999. Reevaluation of the genetic consequences of translocations on deer populations. *Journal of Wildlife Management* 63:327–334.
- LEBERG, P.L., P.W. STANGEL, H.O. HILLESTAD, R.L. MARCHINTON, AND M.H. SMITH. 1994. Genetic structure of reintroduced wild turkey and white-tailed deer populations. *Journal of Wildlife Management* 58:698–711.
- LEBERG, P.L., AND R.C. VRIJENHOEK. 1994. Variation among desert topminnows in their susceptibility to attack by exotic parasites. *Conservation Biology* 8:419–424.
- 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 and Hall, New York.
- MADHAVI, R., AND R.M. ANDERSON. 1985. Variability in the susceptibility of the fish host, *Poecilia reticulata*, to infection with *Gyrodactylus bullatarudis* (Monogenea). *Parasitology* 91:531–544.
- MEFFE, G.K., AND R.C. VRIJENHOEK. 1988. Conservation genetics in the management of desert fishes. *Conservation Biology* 2:157–169.
- MILLER, R.R., AND E.P. PISTER. 1971. Management of the Owens pupfish, *Cyprinodon radiosus*, in Mono County, California. *Transactions of the American Fisheries Society* 100:502–509.
- MINCKLEY, W.L. 1995. Translocation as a tool for conserving imperiled fishes: experiences in the western United States. *Biological Conservation* 72:297–309.
- MINCKLEY, W.L., G.K. MEFFE, AND D.L. SOLTZ. 1991. Conservation and management of short-lived fishes: the cyprinodontoids. Pages 247–282 in W.L. Minckley and J.E. Deacon, editors, *Battle against extinction*. University of Arizona Press, Tucson.
- PARKER, K., R.J. SHEFFER, AND P.W. HEDRICK. 1999. Molecular variation and evolutionarily significant units in the endangered Gila topminnow. *Conservation Biology* 13:108–116.
- PHILIPP, D.P. 1991. Genetic implications of introducing Florida largemouth bass, *Micropterus salmoides floridanus*. *Canadian Journal of Fisheries and Aquatic Science* 48(Supplement 1):58–65.
- QUATTRO, J.M., AND R.C. VRIJENHOEK. 1989. Fitness differences among remnant populations of the endangered Sonoran topminnow. *Science* 245:976–978.
- QUATTRO, J.M., P.L. LEBERG, M.E. DOUGLAS, AND R.C. VRIJENHOEK. 1996. Molecular evidence for a unique evolutionary lineage of endangered Sonoran desert fish (genus *Poeciliopsis*). *Conservation Biology* 10: 128–135.
- REZNICK, D.N., H. BRYGA, AND J.A. ENDLER. 1990. Experimentally induced life-history evolution in a natural population. *Nature* 346:357–359.
- REZNICK, D.N., M.J. BUTLER, F.H. RODD, AND P. ROSS. 1996. Life history evolution in guppies (*Poecilia reticulata*). 6. Differential mortality as a mechanism for natural selection. *Evolution* 50:1651–1660.
- RICHARDS, C., AND P.L. LEBERG. 1996. Evaluation of the effects of bottlenecks on changes in allele frequencies. *Conservation Biology* 10:832–839.
- SAKANARI, J.A., AND M. MOSER. 1990. Adaptation of an introduced host to an indigenous parasite. *Journal of Parasitology* 76:420–423.
- SHEFFER, R.J., P.W. HEDRICK, W.L. MINCKLEY, AND A.L. VELASCO. 1997. Fitness in the endangered Gila topminnow. *Conservation Biology* 11:162–171.
- SPENCER, C.S., J. NEIGEL, AND P.L. LEBERG. 2000. Evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. *Molecular Ecology* 9:1517–1528.
- STEARNS, S.C. 1983. The genetic basis of differences in life history traits among six populations of mosquito-

- fish (*Gambusia affinis*) that shared ancestors in 1905. *Evolution* 38:618–627.
- STOCKWELL, C.A., AND M. MULVEY. 1998. Phosphogluconate dehydrogenase polymorphisms and salinity in the White Sands pupfish. *Evolution* 52:1856–1860.
- STOCKWELL, C.A., M. MULVEY, AND A.G. JONES. 1998. Genetic evidence for two evolutionarily significant units of the White Sands pupfish. *Animal Conservation* 1:213–225.
- STOCKWELL, C.A., M. MULVEY, AND G.L. VINYARD. 1996. Translocations and the preservation of allelic diversity. *Conservation Biology* 10:1133–1141.
- STOCKWELL, C.A., AND G.L. VINYARD. 2000. Life history variation in recently established populations of western mosquitofish (*Gambusia affinis*). *Western North American Naturalist* 60:273–280.
- 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.
- TURNER, B.J. 1984. Evolutionary genetics of artificial refugium populations of an endangered species, the desert pupfish. *Copeia* 1984:364–369.
- VRIJENHOEK, R.C. 1989. Population genetics and conservation. Pages 89–98 in D. Western and M.C. Pearl, editors, *Conservation for the twenty-first century*. Oxford University Press, New York.
- VRIJENHOEK, R.C., M.E. DOUGLAS, AND G.K. MEFFE. 1985. Conservation genetics of endangered fish populations in Arizona. *Science* 229:400–402.
- WALTERS, C.J. 1986. *Adaptive management of renewable resources*. McGraw Hill, New York.
- WILLIAMS, J.E. 1977. Observations on the status of the Devil's Hole pupfish, Hoover Dam Refugium. U.S. Bureau of Reclamation, Environmental Research Center, REC-ERC-77-11.
- WILLIAMS, J.E., D.W. SADA, C. DEACON-WILLIAMS, AND OTHER MEMBERS OF THE WESTERN DIVISION, ENDANGERED SPECIES COMMITTEE. 1988. American Fisheries Society guidelines for introduction of threatened and endangered fishes. *Fisheries* 13:5–11.
- WOLF, C.M., B. GRIFFITH, C. REED, AND S.A. TEMPLE. 1996. Avian and mammalian translocations: update and reanalysis of 1987 survey data. *Conservation Biology* 10:1142–1154.

Received 15 March 2000
Accepted 6 November 2000