

# Translocations and rapid evolutionary responses in recently established populations of western mosquitofish (*Gambusia affinis*)

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(Received 22 June 1998; accepted 28 October 1998)

## Abstract

The response of quantitative traits in translocated populations has not been well explored. Evolutionary shifts in quantitative traits, such as life history characteristics, are of particular interest because of their obvious association with fitness. In a recent survey, Stockwell (1995) examined life history variation of four populations of western mosquitofish (*Gambusia affinis*) that were derived from a common ancestral population 55–58 years earlier. Three life history traits differed considerably among the four sites and appeared to be correlated with local environmental conditions. To test whether these differences were due to plasticity or rapid evolution, fish from the four sites were maintained under common-garden conditions for two generations. After two generations a genetic basis was inferred for two of the three traits (size at maturity and fat content), but not for the third trait (offspring size). Thus, rapid evolution had occurred for two life history traits in these recently established populations. This case of rapid life history evolution may be due to genetic drift and/or natural selection. These data suggest that translocations may lead to rapid evolutionary responses of targeted taxa. Rapid evolutionary responses are of special concern for ‘refuge’ populations that are maintained as a hedge against extinction.

## INTRODUCTION

Considerable resources have been invested in the intensive management of numerous species of rare organisms. These actions, which have included the establishment of wild refuge populations and/or captive populations, have a number of potential evolutionary consequences. For instance, maintenance of genetic variability in managed populations is necessary to allow for future evolutionary potential, yet many managed populations have experienced notable reductions in genetic diversity (Allendorf & Ryman, 1987; Stockwell, Mulvey & Vinyard, 1996). Further, drift and/or selection in managed populations may lead to evolutionary changes in the targeted taxon. For instance, captive populations may face novel selection pressures and undergo selection for various traits (Frankham & Loebel, 1992; Frankham, 1995). Such changes may influence the ability of these populations to respond to natural environments following reintroduction. Novel selection

pressures are not unique to captive populations, since wild ‘refuge’ populations may also experience novel ecological challenges that may lead to rapid evolutionary changes in the targeted taxon (Stockwell & Mulvey, 1998).

Rapid evolution is of most concern when refuge populations are established as ‘genetic replicates’ of a native population as a hedge against extinction. For instance, the Devil’s Hole pupfish (*Cyprinodon diabolis*) is endemic to a small habitat in Death Valley National Monument. Concern for the security of this species has led to the establishment of refuge populations (J. E. Williams, 1977). Such populations would provide stock for reintroduction if the native population was to become extirpated. Under these circumstances, rapid evolution in refuge populations may be an undesirable outcome of this conservation strategy.

Both Mendelian and quantitative traits have been shown to evolve rapidly in introduced populations (Reznick, Bryga & Endler, 1990; Stockwell & Mulvey, 1998). Evolutionary shifts in quantitative traits, such as life history characteristics, are of particular interest because of their obvious association with fitness (for reviews, see Roff 1992; Stearns, 1992). Further, most

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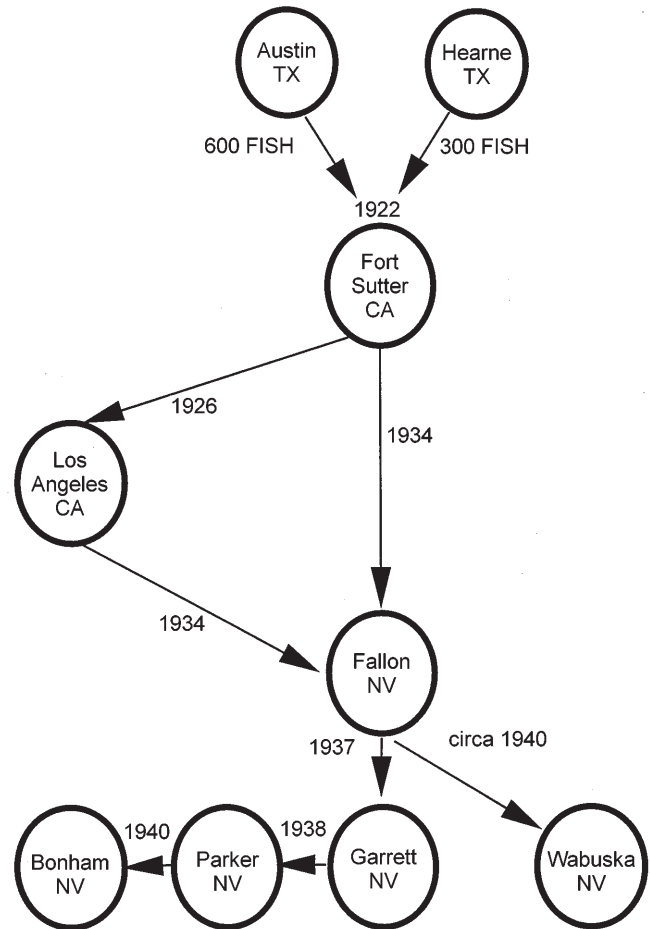
organisms are valued for their phenotypes that include morphological, behavioural and life history traits (Lynch, 1996). As such, these traits contribute to our understanding and appreciation of biodiversity.

Here, we consider how rapid evolutionary responses may occur in populations established by translocation as a conservation measure. We focus on life history traits in recently established populations of western mosquitofish (*Gambusia affinis*), but maintain that this topic is of concern for rare taxa that are actively managed.

Western and eastern mosquitofish (*G. holbrooki*), are native to the south-eastern United States of America, but have been introduced world-wide during this century for mosquito control (Krumholz, 1948; Courtenay & Meffe, 1989). Novel environments now occupied by these species range from cold water lakes in Illinois (Krumholz, 1944) to thermal springs in Nevada (Stockwell, 1995). Thermal springs are perhaps one of the more novel environments experienced by introduced mosquitofish populations, because thermal water sources are virtually absent throughout their native range (Berry, Grim & Ikelman, 1980).

Stockwell (1995) compared female life history traits in four western mosquitofish populations that were descended from native populations in Texas (Fig. 1). Three life history traits showed differences among populations that were associated with the thermal characteristics of their new habitats (Table 1). Females from thermally stable habitats, Bonham and Garrett, matured at intermediate-large sizes, had intermediate-high fat content and large embryos. By contrast, females from a thermally unstable habitat, Wabuska, matured at small sizes, had low fat content and small embryos. Females from Parker, a habitat with intermediate thermal characteristics, matured at intermediate-large sizes, had low fat content and intermediate-large embryos. These data raised the possibility that evolution had occurred in response to local habitats in as short a time as 55 years (110–165 mosquitofish generations: Stockwell, 1995).

To determine if the life history differences measured in the field reflected rapid evolution or phenotypic plasticity, the genetic basis of these life history traits must be determined. Toward this goal, western mosquitofish from all four populations were raised under common-garden conditions in the laboratory. If differences among populations measured in the field persist into the second generation of populations raised in the common-garden, then variation in these traits is assumed to have a genetic basis (Stearns, 1983; Reznick & Bryga, 1987, 1996; Reznick *et al.*, 1990). Alternatively, if differences do not persist under common-garden conditions, then differences observed among field populations reflect phenotypically plastic responses to the environmental differences. These data will help us delineate the likelihood that populations established as a conservation measure may undergo rapid evolution in response to novel selection pressures.



**Fig. 1.** Introduction history of the Nevada study sites (see Stockwell, Mulvey & Vinyard, 1996 for details). The Fort Sutter population was founded in 1922 with approximately 900 fish. The Fallon population was founded in 1934 with fish from Fort Sutter and an additional site in southern California. Subsequently, additional populations were founded from the Fallon site, including Wabuska, Garrett, Parker and Bonham. The number of founders for these latter populations is not known.

**Table 1.** Summary of temperature profiles and life history traits documented for four Nevada mosquitofish populations

Population	Temperature °C	Size at maturity (mm)	Fat content (%)	Typical embryo size (mg)
Bonham	34–36	22–26	11–16	1.6–1.8
Garrett	34	20–21	14–22	1.7–1.8
Parker	28	19–22	8–10	1.4–1.9
Wabuska	12–40	16–18	6–7	1.1

Data are taken from Stockwell (1995).

## BACKGROUND

Approximately 900 western mosquitofish from two localities in central Texas were introduced to Fort Sutter, California in 1922 (Fig. 1) (Stockwell, Mulvey & Vinyard, 1996). Subsequently fish were translocated to

the vicinity of Los Angeles, CA. Fish from the vicinity of Los Angeles and fish from Fort Sutter were used to establish a population near Fallon, Nevada in 1934 (La Rivers, 1962). From this source, a number of populations were founded in northern Nevada in the late 1930s (Fig. 1). In 1937, mosquitofish from Fallon were translocated to Garrett Ranch in the Black Rock Desert. By 1940, mosquitofish had been translocated from Garrett Ranch to Parker Ranch in the northern Smoke Creek Desert and from Parker Ranch to the Bonham Ranch in the southern Smoke Creek Desert (J. Bonham, J. Parker and B. Paschall, pers. comm.: Fig. 1). By 1940, mosquitofish were translocated from Fallon to Wabuska Hot Springs (V. Mills & R. Alcorn, pers. comm.: Fig. 1). All of these populations are at least 50 linear kilometers apart from each other, and lack hydrological connections. Thus, natural gene flow among populations does not occur.

Thermal characteristics varied among these four habitats (Table 1). Bonham and Garrett were characterized by constant high temperatures. Temperatures at Parker were also constant, but of intermediate temperatures (28 °C). Temperatures at Wabuska typically ranged from 25–40 °C, but occasionally winter temperatures dropped as low as 12 °C due to the periodic shut down of hot wells that supported this habitat (Stockwell, 1995).

## METHODS

Pregnant mosquitofish were collected at each of the four Nevada study sites and transported live to the laboratory. The brood stock used to initiate the experimental populations included 14, 21, 21 and 22 wild females from Garrett, Parker, Wabuska and Bonham populations, respectively. Pregnant females were isolated in brooding chambers and allowed to give birth to one brood. Between one and five offspring ( $F_1$  generation) were arbitrarily selected from each brood and introduced into one of four tanks (800-l) representing each population. We constrained the maximum number of offspring per brood to five as an attempt to equalize the representation of the original parental females in subsequent generations (i.e. to maximize the effective population size). Tank temperatures were maintained at approximately 25 °C and fish were fed pellet fish food daily.

Sixteen  $F_1$  females were used from Bonham and Garrett and 15  $F_1$  females were used from Parker and Wabuska. Females were isolated into plastic containers until they gave birth to the  $F_2$  broods. Three  $F_2$  broodmates were randomly selected from each of the  $F_2$  broods and introduced to the experiment at 1 day of age. These  $F_2$  experimental offspring were raised in separate 3.7-l plastic jugs, which were placed in 220-l aquaria (Weeks & Meffe, 1996). A total of eight such aquaria housed 24 plastic jugs. Each jug was submerged to one half of its height and had four mesh-covered windows (4 cm × 8 cm) to allow water exchange. Broodmates were reared in an incomplete, randomized block design with aquaria serving as blocks. Aquaria temperatures were maintained between 25 and 26 °C. The room was lit by broad-

band spectrum fluorescent lights (Vita-lite sunlight simulator bulbs, Durotest Lighting) and placed on a 14:10h light:dark cycle.

Fish were fed daily on a diet that approximated the high diet regime described by Weeks & Meffe (1996). During the first 6 weeks, fish were fed brine shrimp nauplii. Stock solutions of brine shrimp were established daily by adding 1 g of brine shrimp eggs (Argent Chemical Laboratories, Redmond, VA) to 1 l of saltwater and incubating for 48 h. The emergent nauplii were rinsed and concentrated into 250 ml of freshwater. We provided experimental fish with 1.5, 3, 4.5 and 6 ml of this stock solution during days 1–7, 8–14, 15–28 and 29–35, respectively. From days 36–42, fish were fed 6 ml of brine shrimp stock solution or 10.4 ( $\pm$  1.0) mg dry flake food (Prime Flakes Tropical Fish Food, Zeigler Bros., Inc., Gardners, PA) on alternating days. From day 43 onward, fish were fed 10.4 ( $\pm$  1.0) mg of flake food per day.

Body sizes were measured using MorphoSys<sup>®</sup>, a computer image analysis system (Weeks & Meffe, 1996) on day 1, day 22, day at maturity and 14 days after reaching maturity. Animals were measured from the upper lip to the caudal peduncle (standard length, SL) to the nearest 0.01mm. A mean of three measurements was recorded for each animal.

Beginning on day 22, fish were examined every other day for morphological signs of maturity (Weeks & Meffe, 1996). Maturity of females was indicated by the appearance of an abdominal black spot (Constantz, 1989). We report both the average and minimum size at maturity. Two weeks after maturation, fish were preserved in 5% buffered formalin. Fish were not fed on the day that they were preserved.

Egg developmental stage was determined as (i) immature, (ii) mature or (iii) atretic (Wetherington *et al.*, 1989). The five largest mature eggs of the brood were separated from the remainder of the reproductive tissue. Somatic tissue and the five eggs were placed into two separate tared vials. All vials were oven dried at 56 °C for 48 h, placed into a desiccator at 0% humidity for 24 h, and subsequently into a glove box at 0% humidity for 24 h. Samples were then weighed on a Mettler AE240 electronic digital balance to the nearest 0.1 mg (gross weight). Typical weight of the largest eggs was determined by dividing total egg weight by the number of eggs (usually 5 eggs).

To determine fat content, somatic tissue was subsequently subjected to fat extraction. Fish were boiled in petroleum ether for 2 h and rinsed with distilled solvent for 1 h (Meffe & Snelson, 1993). Following fat extraction, each sample was dried and re-weighed following the same weighing procedures previously outlined (net weight). Percent fat content was computed as: ((gross weight – net weight) / gross weight) × 100.

## STATISTICAL ANALYSES

Data were analysed using the General Linear Model (GLM) procedure of the SAS Statistical Package (SAS Institute Inc., 1990). We tested for effects of POPULA-

TION, BLOCK, POPULATION  $\times$  BLOCK and F<sub>1</sub> FEMALE parent within POPULATION. No significant POPULATION  $\times$  BLOCK effects were detected for any of the response variables; therefore, this effect was removed from all models for subsequent analyses. Because a nested design was used, the FEMALE within POPULATION mean square was used as an error term in testing for POPULATION effects. Residuals were tested for normality (Proc Univariate: SAS Institute Inc., 1990). *Post hoc* pair-wise comparisons among all populations were performed using the REGWQ procedure (SAS Institute Inc., 1990).

## RESULTS

Average size at maturity was significantly different among populations (Tables 2 & 3). Wabuska females matured at significantly smaller sizes than Bonham and Parker females (Table 3). Minimum size at maturity also reflected this general pattern. Wabuska females matured

**Table 2.** ANOVA tables for life history traits (using Type III sums of squares)

Effect	d.f.	Mean squares	F ratio	P value
<b>Average size at maturity</b>				
Block	7	0.599	0.66	0.7034
Population	3	7.921	4.24	0.0061
Female (Population)	49	1.866	2.06	0.0176
Error	31	0.907		
<b>Fat content<sup>†</sup></b>				
Block	7	1.850	1.77	0.1287
Population	3	13.714	9.05	0.0001
Female (Population)	50	1.592	1.53	0.1063
Error	31	1.044		
<b>Typical egg weight<sup>‡</sup></b>				
Block	7	0.237	0.66	0.7058
Population	3	0.889	1.44	0.2399
Female (Population)	48	0.663	1.84	0.0415
Error	29	0.362		

<sup>†</sup> MS  $\times 10^3$

<sup>‡</sup> MS  $\times 10^7$

MS, mean square.

at the smallest sizes, followed by Garrett, Bonham and Parker females (Table 3) when raised under common-garden conditions. This pattern was consistent with the field data, where Wabuska females also matured at the smallest sizes (Table 1).

Fat content differed significantly among populations (Tables 2 & 3). Fat content was significantly higher in Wabuska females than in females from the other three populations (Table 3). These data contrasted with the field data. Wabuska females had the lowest fat content among field populations, but the highest fat content under common-garden conditions (Tables 1 & 3).

Embryonic development in mosquitofish is lecithotrophic, with unfertilized eggs having a higher mass than developing embryos (Reznick, 1981). Thus, comparisons between field data on embryo size and common-garden data on egg size can be made, but are of a qualitative nature. No significant differences were detected among populations for egg size in the common-garden data (Tables 2 & 3). By contrast, embryo size varied significantly in the field with Wabuska embryos being significantly smaller than embryos from the other three populations (Table 1).

## DISCUSSION

Translocating populations has become common in the conservation of rare species (J. E. Williams *et al.*, 1988; Minckley, 1995). Early translocations were often conducted in an emergency context as a means of saving species from extinction (see Miller & Pister, 1971; Minckley, Meffe & Soltz, 1991). However, translocations are currently used in a more deliberate manner and typically occur in four contexts: (i) as a mitigation procedure (Allen, 1994), (ii) to augment established populations, (iii) to create 'refuge' populations, and (iv) to re-establish historic populations. Despite the widespread use of translocation as a conservation tool, the evolutionary implications of such actions are not well understood, and concern has been expressed that refuge populations may undergo rapid evolution following translocation (Conant, 1988; Stockwell, 1995).

**Table 3.** Life history characteristics of Nevada mosquitofish populations raised under common-garden conditions for two generations

Life history trait	Population			
	Bonham	Garrett	Parker	Wabuska
Minimum size at maturity (mm) <sup>†</sup>	18.02	17.77	18.24	15.38
Mean size at maturity (mm)	20.33 + 0.32 <sup>a</sup> (n = 23)	19.67 + 0.31 <sup>ab</sup> (n = 25)	20.56 + 0.30 <sup>a</sup> (n = 25)	19.03 + 0.39 <sup>b</sup> (n = 18)
Mean fat content (%)	21.87 + 0.94 <sup>a</sup> (n = 24)	19.00 + 0.92 <sup>a</sup> (n = 25)	20.46 + 0.89 <sup>a</sup> (n = 25)	26.01 + 1.13 <sup>b</sup> (n = 18)
Mean typical egg weight (mg)	1.004 + 0.063 <sup>a</sup> (n = 22)	1.034 + 0.059 <sup>a</sup> (n = 25)	1.157 + 0.057 <sup>a</sup> (n = 25)	1.108 + 0.077 <sup>a</sup> (n = 16)

Data are presented as least square means ( $\pm 1$  standard error of the mean). Significant differences were detected for only mean size at maturity and fat content; means sharing at least one letter were not significantly different. Difference in sample sizes for the various traits was due to a small number of females that did not reach maturity. The differences in sample sizes are reflected by the degrees of freedom presented in Table 2.

<sup>†</sup> Minimum size at maturity is an absolute measure.

In the current study, we documented rapid evolution for mosquitofish life history characteristics. This was facilitated by knowing the introduction histories of these populations, which have been isolated for 55–58 years. Therefore, any genetically-based phenotypic differences among these populations must reflect rapid evolution. Based on evidence from the field study, Stockwell (1995) suggested three life history traits as candidates for rapid evolution: size at maturity, fat content and offspring size. Under common-garden conditions, two generations removed from the field, two of these three traits (size at maturity and fat content) differed among these populations. Because this common-garden design substantially reduces the likelihood of 'carry-over' effects (i.e. 'maternal effects') from the field, we can assume that differences in these two traits are genetically based in these fish populations. Therefore, we conclude that we have documented a case of rapid evolution for these two life history traits.

The other trait found to differ in the field (offspring size) did not differ under common-garden conditions. Thus, the differences described from the field for offspring size must be due to either phenotypic plasticity or to a genotype by environment interaction. These results underscore how observed variation in translocated populations may reflect rapid evolution or simple phenotypic plasticity. We suggest that such variation is of most concern if it reflects evolutionary responses to refuge habitats.

Rapid evolutionary responses may arise by either genetic drift or by adaptive selection. Genetic drift is of special concern for translocated populations because such populations often suffer from reduced genetic variability (Stockwell, Mulvey & Vinyard, 1996). In the current study, all four populations shared a common ancestral stock (Fallon), but the introduction of mosquitofish to Wabuska was independent of the introduction of fish to the other three sites (Fig. 1). Fish were stocked directly from Fallon to both Garrett and Wabuska, however, Bonham and Parker fish were derived from the Garrett population. Therefore, it is conceivable that drift associated with either of the original transfers of fish from Fallon may have led to the divergence of the Wabuska fish from the other three populations.

Alternatively, rapid evolutionary shifts may be due to selection related to local ecological conditions (Stearns, 1983; Reznick *et al.*, 1990). Indeed, divergent selection regimes may explain the observed life history differences among the four Nevada mosquitofish populations. Females at Wabuska were exposed to fluctuating thermal environments where water temperatures ranged from 12–40 °C. Shifts in temperature are likely to influence food availability as well as metabolism in mosquitofish (Vondracek, Wurtsbaugh & Cech, 1988; Meffe, 1991). Also, female mosquitofish at Wabuska showed two signs of stress. First, Wabuska fish had very low fat content in the field (Stockwell, 1995). This low fat level is striking because Wabuska females achieved the highest fat content when raised under common-garden conditions (see below). Second, female mosqui-

tofish at Wabuska were significantly smaller than females from the other three populations (Stockwell, 1995). Because age and size are often correlated in Poeciliids (Reznick *et al.*, 1990), these data suggest that Wabuska females do not live as long as females from other sites. On the other hand, these data may simply reflect relatively lower growth rates of Wabuska females due to local ecological conditions. Collectively, these factors suggest that Wabuska was a comparatively harsh environment. Such harsh conditions may lower both growth rate and average life expectancy of Wabuska mosquitofish, which should select for maturity at a smaller size (Gadgil & Bossert, 1970; Roff, 1984, 1986; Stearns & Koella, 1986), which was indeed found.

Divergent ecological conditions may also explain the results obtained regarding fat content. In the field, Wabuska females had the lowest fat content (Stockwell, 1995), whereas in the common-garden experiment, they had the highest fat content. Apparently, the Wabuska females had a genetic predisposition to store more fat under optimal feeding conditions than the other three populations. One potential explanation for this is that efficient fat storage was necessary at Wabuska because of higher energetic costs or because of food limitation. As mentioned above, the small average size and low fat content of Wabuska females in their native habitat is consistent with the harsh nature of this site (see discussion of countergradient selection in Levins, 1969 and Berven, Gill & Smith-Gill, 1979). Therefore, the observed differences in size at maturity and fat content may reflect responses to divergent selective pressures in the four natural populations. It is interesting to note that Meffe (1991) reported similar life history responses in a population of eastern mosquitofish (*G. holbrooki*) that also experienced an altered thermal environment. This suggests that our data may reflect a generalized response of mosquitofish to novel temperature regimes.

One may ask if rapid evolutionary responses are common for recently established populations. Many studies have reported evidence for rapid evolution in recently established populations. Rapid life history evolution has been recorded for introduced populations of Poeciliids (Stearns, 1983; Reznick *et al.*, 1990) and Salmonids (Hendry, Hensleigh & Reisenbichler, 1998; Kinnison *et al.*, 1998: Table 4). Furthermore, behaviour and morphology have been shown to evolve rapidly in recently established populations (Table 4). As Lynch (1996) has pointed out, these same traits contribute to our definition of biodiversity, and thus should be of primary importance to those interested in conservation of rare species. Additionally, evolutionary implications of translocations may extend beyond the targeted taxa. For instance, native taxa have been shown to evolve in response to recently introduced species (Singer, Thomas & Parmesan, 1993; Carroll, Dingle & Klassen, 1997).

The majority of documented cases of rapid evolution include work on Poeciliids and Salmonids (Table 4). The 'taxonomic' bias in these studies is probably due to the fact that both Poeciliids and Salmonids have been extensively translocated and are generally well studied. Such

**Table 4.** Selected studies that have demonstrated rapid evolution in recently established populations

Species	Generations†	Traits examined	Hypothesized selective agent	Citation
Australian rabbits <i>Oryctolagus cuniculus</i>	125	Morphology Body weight, ear size	Thermal environment	C. K. Williams & Moore (1989)
White Sands pupfish <i>Cyprinodon tularosa</i>	25–50	Phosphogluconate dehydrogenase	Salinity	Stockwell & Mulvey (1998)
Mosquitofish <i>Gambusia affinis</i>	70	Life history traits Male: age, length & growth Female: age, length & growth	Fluctuating and constant environments	Stearns (1983)
Mosquitofish <i>G. affinis</i>	110–165	Life history traits Female: size at maturity, fat storage	Thermal environment	This study
Guppy <i>Poecilia reticulata</i>	7–18	Life history traits Male: age, size Female: age, size	Predator regimes	Reznick <i>et al.</i> (1990)
Guppy <i>P. reticulata</i>	64–96‡	Behaviour	Predator regimes	Magurran <i>et al.</i> (1992)
Sockeye salmon <i>Oncorhynchus nerka</i>	14	Life history traits Time to hatch; time to emerge	Water temperature	Hendry <i>et al.</i> (1998)
New Zealand chinook <i>O. tshawytscha</i>	28	Life history traits Time to hatch	Water temperature	Kinnison <i>et al.</i> (1998)
Soapberry bug§ <i>Jadera aematoloma</i>	374	Beak length	Fruit size of introduced host species	Carroll <i>et al.</i> (1997)
<i>Euphydryas editha</i> §	7	Food preference	Introduced host species	Singer <i>et al.</i> (1993)

We have included only those studies of quantitative traits that demonstrated a genetic basis had been determined in a common environment.

† Andrew Hendry kindly provided estimates of the number of generations of isolation for many of these studies.

‡ Approximately 32 years elapsed between the translocations and the time that this research commenced and we estimated 2–3 generations per year.

§ Evolution was an apparent response by a native species to an introduced plant species.

data may have immediate relevance to conservation for closely related taxa. For instance, numerous species of *Gambusia* are endangered (Minckley *et al.*, 1991) and conservation plans have called for the establishment of new populations of some of these species (Hendrickson & Brooks, 1991).

We suggest that phenotypic responses of newly established populations be examined in other taxa. For instance, pupfish (*Cyprinodon* sp.) are reasonable targets for such studies because they have been extensively translocated (Hendrickson & Brooks 1991; Dunham & Minckley, 1998; Stockwell, Mulvey & Jones, 1998) and many pupfish species are protected (Minckley *et al.*, 1991). Indeed, two studies have documented phenotypic changes in recently introduced pupfish populations. Stockwell & Mulvey (1998) reported rapid evolution at an allozyme locus (phosphogluconate dehydrogenase; Pgdh) in recently established populations of White Sands pupfish (*C. tularosa*). The allele frequencies in two recently established populations varied significantly from allele frequencies in the native parental population. This shift and additional evidence suggested that Pgdh may be under selection by salinity (Stockwell & Mulvey, 1998). Thus, rapid evolution may ultimately lead to a refuge population that is not adapted to its native envi-

ronment. This issue is of particular concern, because conservation plans call for the establishment of at least one additional refuge population of White Sands pupfish (Stockwell, Mulvey & Jones, 1998).

In another example, J. E. Williams (1977) reported that a recently established refuge population of the endangered Devil's Hole pupfish (*Cyprinodon diabolis*) differed in morphology from the parental stock at Devil's Hole. Unfortunately, this population was recently extirpated, therefore it is not possible to assess whether the change in morphology was due to plasticity or rapid evolution. However, this case points out the need to assess the basis for phenotypic changes in populations established in the context of conservation.

The above documented cases of rapid evolution have been derived from circumstances in which habitats varied in obvious and measurable parameters. However, translocation efforts are typically made to ensure that the 'refuge' habitat is representative of the targeted taxa's native habitat. For this strategy to be successful, extensive ecological information will be required from both the native and targeted 'refuge' habitats. We suggest that even under the 'best case' scenarios, one or more important ecological factor(s) is likely to differ between the native site and the refuge site, which could potentially

lead to rapid evolution in the refuge site. However, the impact of such change on the reintroduction success of these refuge populations remains to be examined.

It is likely that translocations will continue to play an important role in the conservation of rare species. Over 80% of recovery plans for endangered and threatened fish species call for the use of some form of translocation (J. E. Williams *et al.*, 1988). In emergency contexts, managers will not have the 'luxury' to consider such issues as whether refuge populations may undergo rapid evolutionary responses to novel selection pressures. However, our results suggest additional caution in the use of translocation as a mitigation option. We argue that our findings provide additional impetus for the protection of species in their native range, and for better understanding of both the basic biology and ecology of protected species.

## ACKNOWLEDGEMENTS

We thank S. Diaz-Conde, S. Lee, T. Miettunen and A. Yuan for assistance with the data collection. G. Meffe graciously provided laboratory space, supplies and logistical support. We are appreciative of constructive comments that were provided by P. Brussard, P. Dixon, M. Draney, K. Garrett, K. Gubista, G. Hoelzer, S. Jenkins, K. Kandl, W. Longland, G. Meffe, M. Mulvey, G. Vinyard and two anonymous reviewers. Thanks to A. Hendry for sharing an unpublished manuscript. This work was funded by the Biodiversity Research Center at the University of Nevada Reno and a Sigma-Xi Grant to C.A.S. and by contract DE-AC09-76SR00819 between the U. S. Department of Energy and the University of Georgia's Savannah River Ecology Laboratory.

We dedicate this paper to the memory of Dr Gary L. Vinyard, teacher, mentor and friend.

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