

USING SURVIVAL ANALYSIS TO STUDY TRANSLOCATION SUCCESS IN THE GILA TOPMINNOW (*POECILIOPSIS OCCIDENTALIS*)

FRANCES J. SHELLER,^{1,4} WILLIAM F. FAGAN,^{1,5} AND PETER J. UNMACK^{2,3}

¹Department of Biology, University of Maryland, College Park, Maryland 20740-4415 USA

²School of Life Sciences, Arizona State University, Tempe, Arizona 85287-4601 USA

³University of Oklahoma Biological Station, HC 71 Box 205, Kingston, Oklahoma 73439-9738 USA

Abstract. Translocation, the intentional release of captive-propagated and/or wild-caught animals into the wild in an attempt to establish, reestablish, or augment a population, is a commonly used approach to species conservation. Despite the frequent mention of translocation as an aid in threatened or endangered species recovery plans, translocations have resulted in the establishment of few sustainable populations. To improve the effectiveness of translocation efforts, it is essential to identify and adopt features that contribute to successful translocations. This study analyzed 148 translocations of the endangered Gila topminnow (*Poeciliopsis occidentalis*) to identify various factors that have significantly influenced translocation success. We quantified success as the “persistence time” of translocated populations and used survival analysis to interpret the role of several factors. The following factors affected persistence times of translocated populations: season in which the fish were translocated, habitat type of the translocation site, and genetic origin of the fish stocked. In general, factors associated with stocking, the population stocked, and the site of translocation can significantly affect the persistence of translocated populations and thus increase the probability of translocation success. For Gila topminnow, future translocations should be undertaken in late summer or fall (not early summer), should occur into ponds (not streams, wells, or tanks), and should generally utilize individuals from genetic lineages other than Monkey Spring. For other species, a key lesson emerging from this work is that life history attributes for each translocated species need to be considered carefully.

Key words: endangered fish; false absence; genetic lineage; Gila topminnow; habitat type; *Poeciliopsis occidentalis*; population persistence estimates; season; species conservation; sporadic monitoring; survival analysis; translocation.

INTRODUCTION

Extinction and translocation

Anthropogenic degradation of natural habitats has increased species extinction rates and reduced biological diversity worldwide. The situation is especially bad in freshwater systems (Palmer et al. 2004), where the development of land and regional water resources has fragmented populations, increasing their vulnerability to extinction (Fagan et al. 2002, 2005). This fragmentation can result in the restriction of natural dispersal, a mechanism that expands populations, increases species ranges, and maintains genetic diversity in freshwater fish (Minckley 1999). In the past century, at least 20 freshwater fish species in the western United States have become extinct (Miller et al. 1989). Fifteen years ago, two-thirds of the remaining native fish species were of special concern (Williams et al. 1989), and the situation

is believed to be far worse today. Among extant fishes native fishes of the western United States and northern Mexico, populations of short-lived fishes (living ≤ 3 years) are more prone to extinction than are similar-sized populations of long-lived species (Hendrickson and Brooks 1991).

Conservation efforts to minimize local extirpations caused by human manipulation have been implemented in many freshwater systems (Minckley and Deacon 1991, Young and Guenther-Gloss 2004). One commonly used conservation tool is translocation, the intentional release of captive-propagated and/or wild-caught animals into the wild in an attempt to establish, reestablish, or augment a population (Griffith et al. 1989, Minckley 1995). Translocations of endangered native species have become increasingly popular (Groombridge et al. 2004) because endangered species translocations mimic natural dispersal, resulting in the potential for increased total population size, increased dispersion, and the maintenance of genetic diversity (Minckley 1995).

Despite their frequent use and prominence in species recovery plans, translocations have had limited success in creating self-sustaining populations. Griffith et al. (1989) and Wolf et al. (1996) surveyed 421 translocation programs and found that fewer than half of the

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⁴ Present address: Graduate Group in Ecology, 1 Shields Avenue, University of California, Davis, California 95616-8628 USA.

⁵ Corresponding author. E-mail: bfagan@glue.umd.edu

translocation efforts are successful. In their multispecies reviews of translocation efforts, Griffith et al. (1989) and Wolf et al. (1996) found that primary factors associated with translocation successes were: (1) habitat quality, (2) location of release area (e.g., inside or outside the species native range), (3) number of animals released, (4) duration of translocation program, and (5) reproductive traits. Additionally, behavioral traits of the translocated species can influence translocation success (Armstrong and Craig 1995, Clarke and Schedvin 1997, Van Zant and Wooten 2003), demonstrating that species-specific attributes must be considered when determining factors associated with translocation success.

In a focused survey, Hendrickson and Brooks (1991) analyzed the outcomes of almost 500 translocations of 40 short-lived fish taxa reestablished into wild habitats of the western United States. Hendrickson and Brooks (1991) reported that they were unable to characterize the "success" of translocated stocks consistently because the translocations were assessed using widely divergent and generally qualitative criteria. This inability to identify successful translocations highlights the need for more in-depth examination of translocation success using consistent, quantitative criteria.

Hendrickson and Brooks (1991) reported that 47% (230 out of 490) of translocation events they assessed were associated with Gila topminnow (*Poeciliopsis occidentalis*). After its listing as an endangered species in 1967, the Gila topminnow has been translocated into >178 wild locations (Voeltz and Bettaso 2003), representing a wide array of habitat types, ecological communities, and stocking conditions. The availability of such a large amount of translocation data for a single species provides a unique opportunity to investigate the factors that determine translocation success, free from the variability that results from interspecific differences. Here we ask what factors (e.g., stocking conditions, environmental settings) best predict translocation success for Gila topminnow, where success is quantified by a standardized metric: persistence time of a translocated population. This perspective represents a substantial departure from past analyses of translocations that typically dealt with success only as a categorical or ordinal variable.

Gila topminnow

Conducting this analysis requires statistical techniques specifically designed for analyses of persistence time data (specifically, survival analyses via Kaplan-Meier regressions). The Gila topminnow is a small (<50 mm), viviparous poeciliid fish native to the Sonoran Desert of the southwestern United States. In addition, it is the northernmost member of its genus (Meffe et al. 1983) and the only member of the family Poeciliidae native to the Gila River drainage (a major tributary of the Colorado River that drains much of Arizona, western New Mexico, and parts of Sonora, Mexico; Minckley 1973). Gila topminnows tolerate a wide range

of physicochemical conditions (e.g., variable temperatures, water chemistries, and current velocities), and the species historically thrived in diverse habitats of large streams and rivers including the Gila, Salt, Santa Cruz, San Pedro, and other minor tributaries (Minckley 1973) at elevations below 1600 m.

The Gila topminnow, like most poeciliids, has a capacity for rapid population growth. This trait is indicative of species that are excellent at colonizing new habitats (Minckley 1999), and should be advantageous to translocation efforts. For example, the life span of Gila topminnows is approximately one year and they experience an early onset of reproductive maturity at temperatures commonly experienced in the field. These fish may superfetate (simultaneously carry more than one brood) and reproduce throughout the year. Gestation periods range from 24 to 28 days and adults produce 5–20 young per brood (Minckley 1999). Gila topminnows are omnivores, eating a mixture of small invertebrates, detritus, and algae (Minckley 1973).

Federally classified as endangered since 1967 (USFWS 1984), the Gila topminnow has declined from what was "... one of the commonest fishes in the southern part of the Colorado River drainage basin..." (Hubbs and Miller 1941), to persisting in fewer than 11 isolated natural populations (Minckley 1999, Weedman 2000). This rapid decline (spanning 1941–1967) can be attributed to a wide variety of interactive factors related to human development, including: (1) construction of dams and other water projects that dewatered river channels and blocked natural dispersal avenues; (2) the introduction of nonnative predatory and competitive fishes (e.g., *Gambusia* spp.); (3) the drainage of wetlands; and (4) the desiccation or alteration of backwaters, streams, springs, and cienegas as a result of watershed, vegetation, hydrologic, and geomorphologic changes (Minckley 1999). Current management of the Gila topminnow consists of a combination of monitoring natural stocks, habitat manipulations to recover declining native populations, assessment and amelioration of adverse human activities, stocking and monitoring new populations within the natural range, control and removal of nonnative species, maintenance of stocks at universities, museums, and hatcheries, and an ongoing program of basic research (Minckley et al. 1991, USFWS 2000).

MATERIALS AND METHODS

Database construction

We compiled a Gila topminnow translocation database (Appendix) from a variety of sources, including federal and state recovery plans, technical reports, status reports, and memoranda. Gila topminnow conservation is coordinated by the U.S. Fish and Wildlife Service and the Arizona and New Mexico Game and Fish Departments. A wide variety of state, federal, tribal, local, and private entities are involved in the ongoing recovery effort.

TABLE 1. Stratification variables, their respective levels, and frequencies within the full database of 148 Gila topminnow (*Poeciliopsis occidentalis*) translocations.

Strata	Translocation factors						
	Translocation details		Site-specific factors		Population-specific factors		Presence of other species
	Year stocked	Season of stocking	Habitat type	Water source of habitat	No. fish stocked	Genetic origin	
First	≤1981 (20)	Jan–May (31)	streams (81)	spring fed (85)	<200 (14)	Bylas, Cienega, or Sharp Springs (12)	0 after stocking (28)
Second	1982–1983 (104)	Jun (79)	ponds and lakes (15)	surface fed (54)	200–299 (62)	Monkey Spring (130)	1 (51)
Third	≥1984 (24)	Jul–Dec (38)	wells and tanks (52)	well fed (9)	300–800 (29)	NA	2 (16)
Fourth	NA	NA	NA	NA	>800 (27)	NA	>2 (11)
Missing	NA	NA	NA	NA	(16)	(6)	(42)

Notes: Each column is to be read independently because the row labels under “Strata” apply separately to each of the seven translocation factors. This means that each of the 148 translocations could be characterized by up to seven traits, but some were missing. Sample sizes (number of translocations) are given in parentheses. In “Year stocked,” ≤1981 means during or before 1981; ≥1984 means during or after 1984. NA indicates that data are not applicable.

We focused on 148 fish translocations into 134 natural habitats (Table 1), ignoring numerous translocations in which Gila topminnows were either (1) stocked into aquaria, refugia on university campuses, or other human dominated habitats; or (2) where basic data about translocations (e.g., year) were not available. By restricting the data set, we were able to focus on the effectiveness of well-characterized translocations in fostering self-sustaining populations. Our database included those translocations analyzed by Brooks (1985, 1986), who examined a data set for 50 Gila topminnow translocation sites for which detailed physicochemical details were available, and found that drainage area, elevation, cover type, and dissolved oxygen were useful in distinguishing between successful and failed translocations. However, other sources of variation among translocations, such as those pertaining to the fish themselves rather than to the sites, were not considered in his analysis. Likewise, the suites of physicochemical characteristics analyzed by Brooks (1985, 1986) were not available for the full data set.

Our compiled data set of 148 translocations included the number of fish stocked, the genetic origin of the fish in the translocated stock, and the month and year in which a particular translocation was undertaken. Other details concerning attributes of the translocation sites (such as habitat type and water source) also were often available. Overall, the database was sufficiently complete that we could examine the impacts of seven core variables on persistence (Table 1). However, not all variables were available for all of the translocations. Consequently, sample sizes for the statistical analyses varied considerably (i.e., from 148 to 106), depending on what population or site attributes were included in the statistical models (Table 1).

After stocking fish into wild sites, the agencies participating in Gila topminnow conservation variously monitored translocated populations to assess population persistence. Monitoring activities, which were conducted regularly for some sites, but only sporadically for others, consisted of visual inspections of the sites, assessments of habitat conditions, and identification of the fish species present (if any). Each site was sampled using dip nets, seines, minnow traps, or backpack electrofishers, with the intent to being to maximize the probability of detecting Gila topminnow (Voeltz and Bettaso 2003). The 15 translocated populations persisting in 2003 (Voeltz and Bettaso 2003) were deemed extant for the purposes of our analyses.

At each of 14 sites, managers conducted two or more translocations at least one year apart. In those 14 cases, we treated the sequential translocations as independent events; thus, for each site, persistence or failure of the first translocation was evaluated prior to any consideration of the effects of subsequent translocations. In the statistical analyses (SYSTAT version 10.2), this approach meant that the persistence estimate of the first translocation into a site was the time gap between the first and second translocations (Fig. 1). However, if the population from a previous translocation was extant at the time of a subsequent translocation, the population size after the subsequent translocation was the sum of the preexisting and the stocked populations (if both were known).

Drawing upon general conservation theory and the specific life history of Gila topminnow, we identified four classes of factors that potentially might affect population persistence. The first class focused on details of the translocation activities and included two factors: the year in which the translocation occurred and the seasonal timing of translocation. We separated trans-

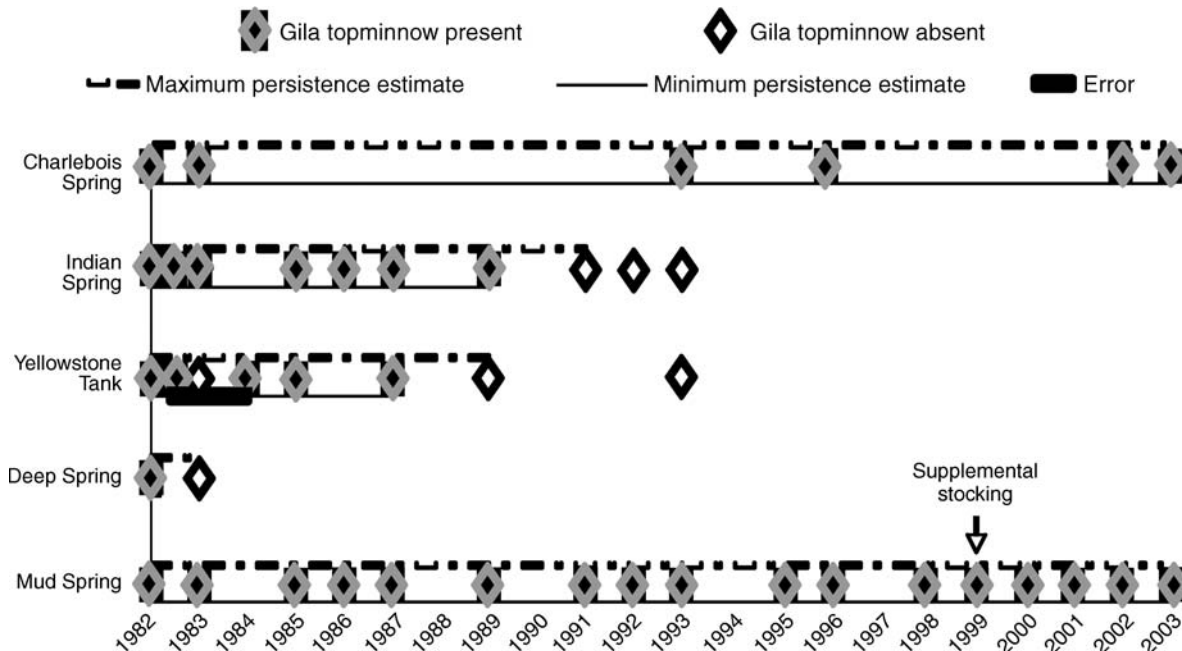


FIG. 1. Examples of how minimum and maximum population persistence times for *Gila topminnow* (*Poeciliopsis occidentalis*) were calculated from sporadic monitoring data. All sites listed were stocked in 1982.

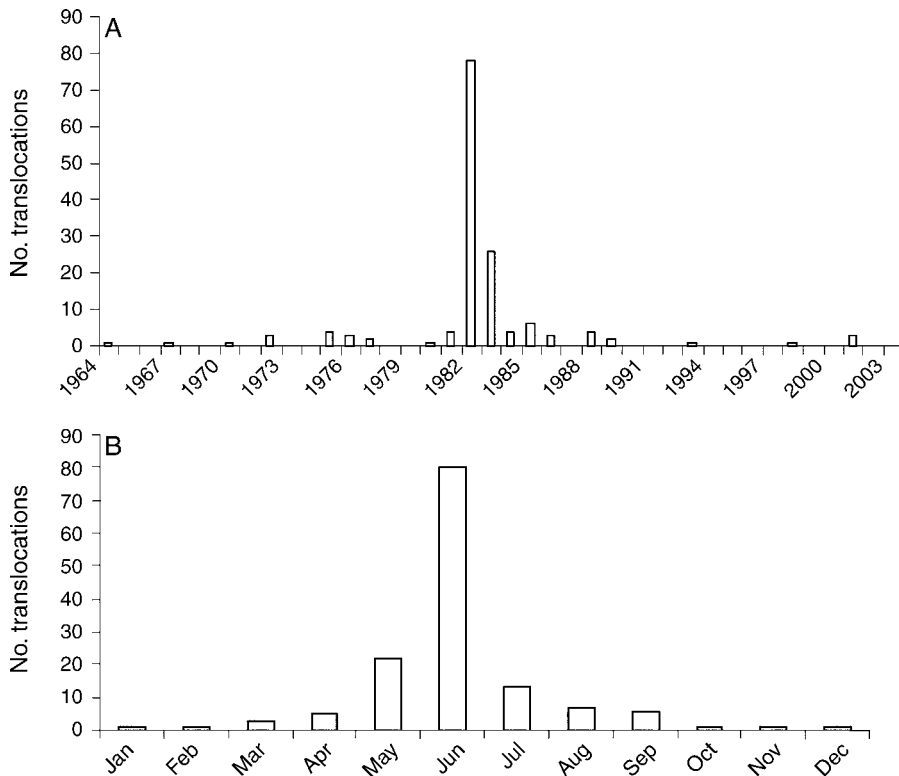


FIG. 2. Breakdown of the frequency of translocation efforts for *Gila topminnow* as functions of (A) year and (B) month.

locations ($N = 148$) into three year groups chosen from the data set (Fig. 2A): (1) 1964–1981 ($N = 20$), (2) 1982–1983 ($N = 104$), and (3) 1984–2002 ($N = 24$). We also separated stocking season into three periods because seasonal timing has been shown to be critical to success and/or failure of other conservation-related activities (e.g., Pardon et al. 2003, Young and Guenter-Gloss 2004): (1) January–May, (2) June, and (3) July–December (Fig. 2B).

A second class of factors addressed site-specific traits. Here we considered the habitat type where translocations occurred (e.g., pond, spring, creek) and the water source of the translocation site (e.g., spring-fed, surface-fed, well-fed). Historically, *Gila topminnow*s preferred warm waters with a slow current and abundant aquatic vegetation, but the species can survive in a variety of habitats (Minckley 1999). We note that lakes, in the proper geomorphological sense, are effectively absent from the historic geographic range of the *Gila topminnow*. Thus, with only two exceptions (Watson Lake and Willow Creek Reservoir), the habitat type category “ponds and lakes” refers to a collection of small water bodies (variously named ponds, pools, or lakes on maps) formed by a small dam or impoundment across a small natural watercourse. The issue of “natural watercourse” is a key distinction separating sites in this category from an alternative category “wells and tanks.” The Appendix categorizes each translocation with regard to this and other factors.

The third class that we considered included population-specific factors that might influence population persistence via demographic effects. We considered two factors within this class: initial population size and initial genetic diversity, because both initial population size (Lande et al. 2003, Matson et al. 2004) and initial genetic diversity of the translocated individuals (Meffe 1986, Hartl and Clark 1997) previously have affected population success in translocated populations. Genetic origin or, more specifically, the genetic diversity of the translocated individuals, was a factor of special interest in our analysis because of population genetic concerns about fish from one of the primary source populations, Monkey Spring. In lab studies, Quattro and Vrijenhoek (1989), found that fish from the environmentally stable habitat comprising Monkey Spring lacked allozyme variation and were less fit (in terms of survival, growth, early fecundity, and developmental stability) than fish from the more environmentally variable Sharp Spring population. However, Sheffer et al. (1997) disputed these results because they were unable to find similar differences in fitness. Thus, we used microsatellite and MHC (major histocompatibility complex) analyses (Hedrick et al. 2001) to identify translocations of Monkey Spring lineage.

Lastly, we wanted to explore whether the presence of other species influenced persistence time of translocated populations. In particular, given the widespread concern regarding impacts of nonnative fishes on native desert

fishes, in general (Minckley et al. 1991, Unmack and Fagan 2004), and on *Gila topminnow*, in particular (Minckley 1999), we initially planned to explore whether nonnative fish species (e.g., *Gambusia* spp.) at the translocation site influenced persistence time of a translocated population. However, the database did not include enough cases in which nonnatives and *Gila topminnow* temporally co-occurred at a translocation site to analyze the potential impacts of any individual nonnative species or suite of ecologically similar nonnative species. Management reports attribute losses of three translocated populations to *Gambusia* (Voeltz and Bettaso 2003). As an alternative approach, we conducted survival analyses to explore whether other species, regardless of identity, influenced translocation success: we lumped native and nonnative species together to calculate overall fish species richness at each translocation site.

Estimating persistence times with sporadic monitoring data

A translocated fish population subject to routine monitoring would have a persistence time that extends from the date of initial stocking until the population is extirpated. However, in the absence of annual monitoring, it is difficult to pinpoint extinction time of a population that would be observed extant one year but found to be extirpated some years later (Fig. 1). In this case, the true end point of the translocated population’s “lifetime” would be somewhere between two monitoring visits. Calculated across translocation sites within the *Gila topminnow* data set, the time between monitoring visits was 6.6 ± 6 yr (mean \pm SE). Given the wide uncertainty in persistence times that is associated with such sporadic monitoring, we calculated two persistence estimates for each translocated population (Fig. 1). The first estimate, or minimum population lifetime, assumes that the population became extirpated immediately after the last visit in which the population was observed extant. The second estimate, or maximum population lifetime, assumes that the population became extirpated immediately before the monitoring visit during which the population was observed extinct. Although the minimum population lifetime estimate is the more conservative of the two choices, and is more often used as an indication of population persistence (Hendrickson and Brooks 1991), our use of two estimates of persistence time provides alternative, complementary perspectives on translocation success. In the event that a translocated population was never observed extant after its initial stocking, we assumed that the minimum population lifetime was two weeks. (An assumption of a nonzero lifetime was necessary in the statistical analyses that we conducted, and we chose two weeks because it was quite short relative to the database-wide median interval of six years between the time of stocking and the time of first monitoring.)

TABLE 2. Count of translocations stratified by the characteristics that significantly affect population persistence for the 121 translocated populations with the most complete information.

Genetic origin and habitat type	Season	Frequency
Other than Monkey Spring		
Streams	Jan–May	2
Streams	Jul–Dec	5
Ponds and lakes	Jul–Dec	1
Wells and tanks	Jul–Dec	1
Monkey Spring		
Streams	Jan–May	10
Streams	Jun	38
Streams	Jul–Dec	14
Ponds and lakes	Jan–May	1
Ponds and lakes	Jun	6
Ponds and lakes	Jul–Dec	4
Wells and tanks	Jan–May	5
Wells and tanks	Jun	29
Wells and tanks	Jul–Dec	5

Note: The table is read such that the first two columns together define a suite of translocation details and the last column provides the number of translocations matching that suite of traits.

Because topminnows may be difficult to observe (S. Stefferud, *personal communication*), the Gila topminnow recovery plan (USFWS 1984, Weedman 2000) calls for a translocation site to be revisited repeatedly even after a monitoring visit has deemed the fish to be “absent.” In the context of our analysis, this provides a unique opportunity to assess the error rate of presence–absence monitoring data for this species.

Survival analysis

We used survival analysis (Kalbfleisch and Prentice 1980, Klein and Moeschberger 1997) to characterize persistence times of translocated Gila topminnow populations and to determine how those persistence times depended on differences between sites or translocation efforts. Specifically, we used stratified Kaplan-Meier regression to characterize the persistence times of the translocated populations. Kaplan-Meier regression (also known as product-limit regression) is a non-parametric technique for analyzing survivorship data, such as those derived from longitudinal studies of medical patients. In our case, we treated translocation efforts as the “individuals” and monitored how long they persisted. The hazards model h is written

$$h(t) = b(t)\exp(\beta) \quad (1)$$

where t is time since the start of the translocations (all populations are rescaled to start at time 0), b is the nonparametric baseline hazard function, and coefficient vector β represents the unique contributions of the different strata. The underlying assumption is that the number of individuals in a collection (i.e., translocation efforts) rescaled to a common starting time should decay over time. The rate of decay of the collection is dependent upon trait variation among individuals within

the collection and how those traits influence the likelihood of an individual failing. The label “stratified” in stratified Kaplan-Meier regression means that we can use survival analysis to distinguish whether the distributions of persistence times differ between subsets (“strata”) of the Gila topminnow translocation database (e.g., pond vs. spring habitats, early-summer stocking vs. late-summer stocking), and if so, to quantify how those respective survival functions differ. In our survival analysis, all 15 populations that were extant in 2003 were treated as right-censored data, meaning that the population persistence time is known to be greater than a specified number, but its true value is not known (Klein and Moeschberger 1997).

Using the Tarone-Ware log-rank task, we determined the chi-squared statistic and significance level for each stratified Kaplan-Meier regression. A P value < 0.05 implies that different strata within a given factor have significantly different impacts on persistence of translocated populations. We conducted separate survival analyses on the data sets of minimum and maximum population lifetimes. We considered a factor to be significant if either the minimum or maximum lifetime survival analysis identified it to be significant. Naturally, those factors that significantly influence both maximum and minimum lifetimes for translocated populations are even more compelling.

Looking across the seven factors considered a priori as sources of variation in Gila topminnow persistence times (Table 1), it was clear that the database suffered from some intrinsic imbalances with regard to how the cases fell out across strata. This was a potential problem because it meant that, if we were not careful about how we defined the strata within each factor, effects from different factors might be confounded. The same issue also meant that survival analyses based on cross-classifications across factors would provide limited insight due to limited sample sizes. Given these limitations, we opted to restrict the data set available for each stratified Kaplan-Meier regression to a smaller subset of translocation events that were comparable except for the one factor that we considered as a stratification variable (Table 2). In applying this filtering approach, we reasoned that if the same trend is observed via stratified regression using both the limited data set and the original, full-size data set, then the trend is more likely to be dictated by the variable under investigation and less likely to be the result of some hidden bias in the data set. We employed two such filtered analyses. First, to test the importance of habitat type while controlling for any effects of other variables that our analyses indicated were important, we restricted the data set to translocations that took place in June, and used fish that originated from Monkey Spring (thus eliminating variation in seasonality and genetic origin). Second, after restricting ourselves to these translocations, we tested for a difference in season of stocking.

RESULTS

Estimating an error rate for presence-absence monitoring

The Gila topminnow was recorded as absent during monitoring of nine of the 148 recorded translocations, but it was observed at all nine sites during a subsequent visit. Such erroneous results most likely resulted because of faulty monitoring and resulted in a “false-absence” rate of 6%. We treated all of these cases as if the fish were actually present throughout the intervening periods between monitoring visits, and adjusted our calculations of population minimum and maximum lifetimes accordingly before conducting other analyses (Fig. 1).

Characterizing persistence times of translocated populations

The majority of translocated populations failed rapidly, with 50% (maximum persistence estimate) to 70% (minimum persistence estimate) of populations failing within the first five years after stocking (Fig. 3).

All four classes of factors (translocation details, site-specific factors, population-specific factors, presence of other species) were associated with changes in the persistence time of translocated populations of Gila topminnow. However, within each class, only one or a few factors were significantly associated with changes in either maximum or minimum persistence time of the translocated populations, and only two factors were significantly associated with changes in both maximum and minimum persistence time. We discuss results for each of the four classes of factors in turn.

In the first class of factors, translocation details, we were able to consider the effect of the seasonal timing of the translocation activity and the year in which it was conducted. When we used the maximum persistence estimate, the year of stocking was associated with a change in the persistence time of a translocated population (Fig. 4A). Specifically, those translocations stocked before 1982 survived longer than those stocked during 1982–1983 or those stocked after 1983 (averaging 12 years vs. 5 years and 7 years, respectively; $N = 148$ translocations; $\chi^2 = 19.64$, $df = 2$, $P < 0.001$). However, this result may have been confounded with a (non-significant) tendency toward systematic variation in time between censuses (7.8 ± 1.2 yr; mean \pm SE.), prior to 1982 vs. 5.5 ± 0.4 yr for the period 1984–2002). We found no association of year of stocking with the minimum persistence times (Fig. 4B). In contrast, for both maximum and minimum persistence times of populations, populations translocated during July–December persisted longer than did those stocked during any of the other time periods (Fig. 4C, D). For example, when considering the maximum persistence estimates, populations stocked during July–December survived, on average, for 9 years, whereas populations stocked during January–May survived, on average, for 5 years ($N = 148$ translocations; $\chi^2 = 9.92$, $df = 2$, $P = 0.007$; Fig. 4C).

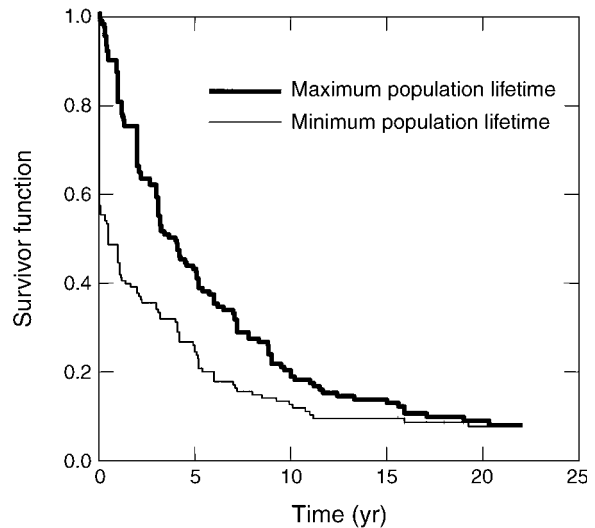


FIG. 3. Survival plot showing minimum and maximum estimates of population persistence for 148 translocations of Gila topminnow. The initial steep drop in the survivor curve for minimum persistence estimates is due to the large number of translocations for which there is no evidence that any of the stocked animals survived beyond the initial translocation.

In the second class of factors, site-specific attributes, both habitat type and water source were associated with changes in population persistence. For both maximum and minimum persistence time, populations translocated into ponds and lakes persisted significantly longer than populations translocated into either streams or wells and tanks (Fig. 5A, B). For example, using maximum persistence time, translocations into ponds and lakes survived, on average, for 14 years, whereas populations stocked in streams persisted for 6 years and those stocked in wells and tanks persisted, on average, for four years ($N = 148$ translocations; $\chi^2 = 16.15$, $df = 2$, $P < 0.001$; Fig. 5A). When considering differences in water source at the translocation site (i.e., using strata of surface-fed, spring-fed, and well-fed) for minimum persistence time, we found that populations at sites that were spring-fed persisted longer than those at sites that were surface-fed or well-fed (5 yr vs. 1 yr and 4.5 yr, respectively; $N = 148$ translocations; $\chi^2 = 8.98$, $df = 2$, $P = 0.011$; Fig. 5D). For maximum persistence time estimates, however, the different types of water sources had no significant effect (Fig. 5C).

Of the population-specific factors that we considered, we found that only the genetic source of the translocated individuals was associated with variation in population persistence times. In particular, using the minimum population lifetime estimates, we found that translocated populations stocked with fish from sources other than Monkey Spring tended to persist longer than translocated populations stocked with fish originating from Monkey Spring (12 yr vs. 4 yr, respectively; $N = 142$ translocations; $\chi^2 = 6.69$, $df = 1$, $P = 0.01$; Fig. 6B). A similar, although nonsignificant, trend was observed

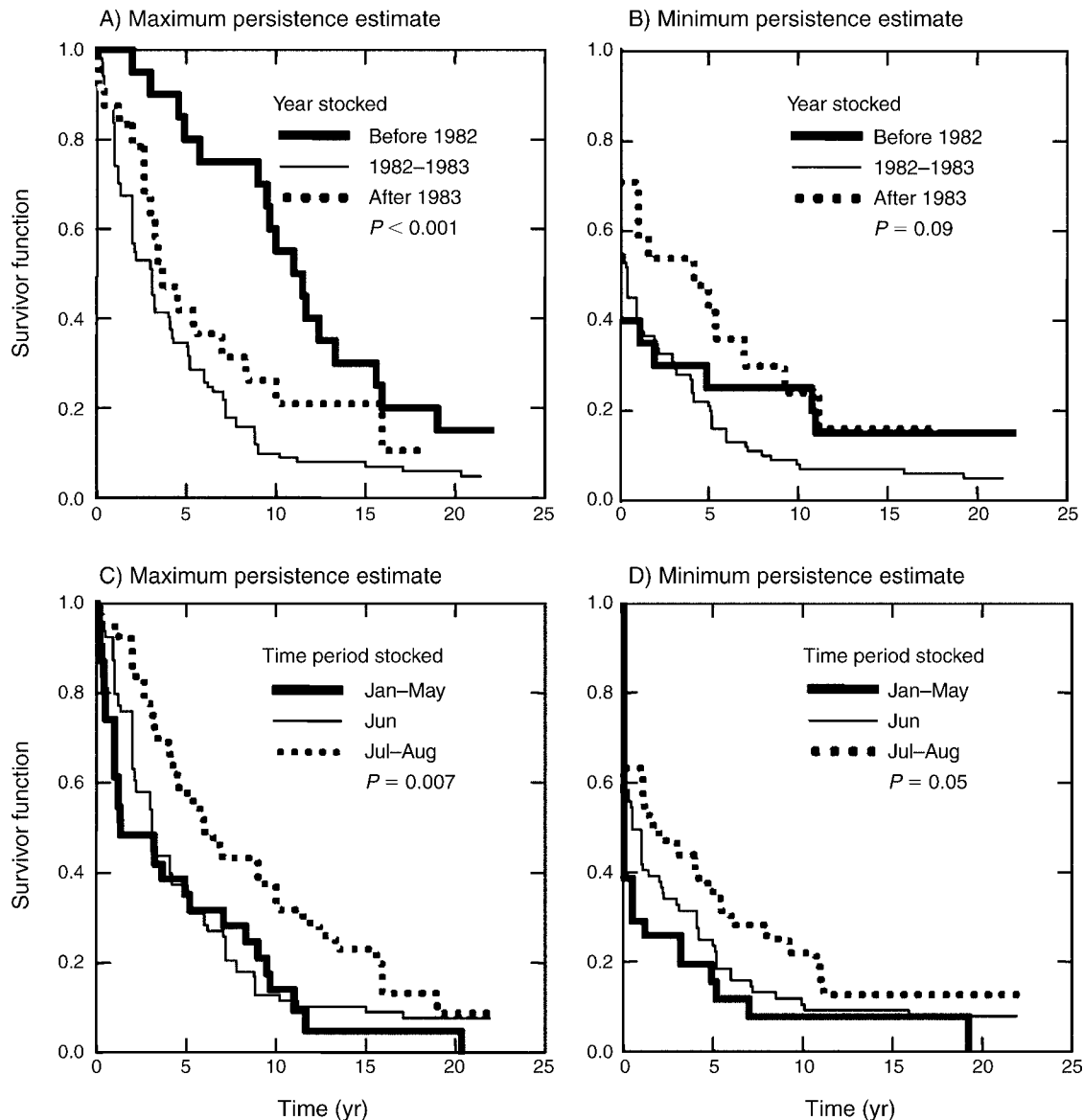


FIG. 4. Survival plots showing how the stratification variables year of stocking (A and B) and season of stocking (C and D) influenced maximum and minimum population persistence times for translocated populations of Gila topminnow.

using the maximum population lifetime estimates (Fig. 6A). In contrast, the number of individuals translocated into a site was not significantly associated with how long that population would persist.

When analyzing the fourth class of factors (the presence of other species), we found no association between persistence times and the total number of other fish species (both native and nonnative) present at a translocation site.

Our analyses of the “filtered” subsets of the translocation database reinforced the importance of the factors identified as important in the analyses above. First, when restricting ourselves to translocations that took place in June and that used fish that originated

from Monkey Spring (thus eliminating variation in seasonality and genetic origin) we found that, even with these constraints, habitat type was still significantly associated with changes in both minimum and maximum lifetime persistence times. For both metrics, translocated populations located in ponds and lakes persisted approximately five times longer than did translocations into either streams or wells and stock tanks (17 years vs. 3 years and 4 years, respectively; $N = 63$ translocations; $\chi^2 = 12.05$, $df = 2$, $P = 0.002$; Fig. 7A, B). Second, restricting ourselves to translocations stocked into streams using fish originating from Monkey Spring, we found once again that translocations during July–December survived better than other transloca-

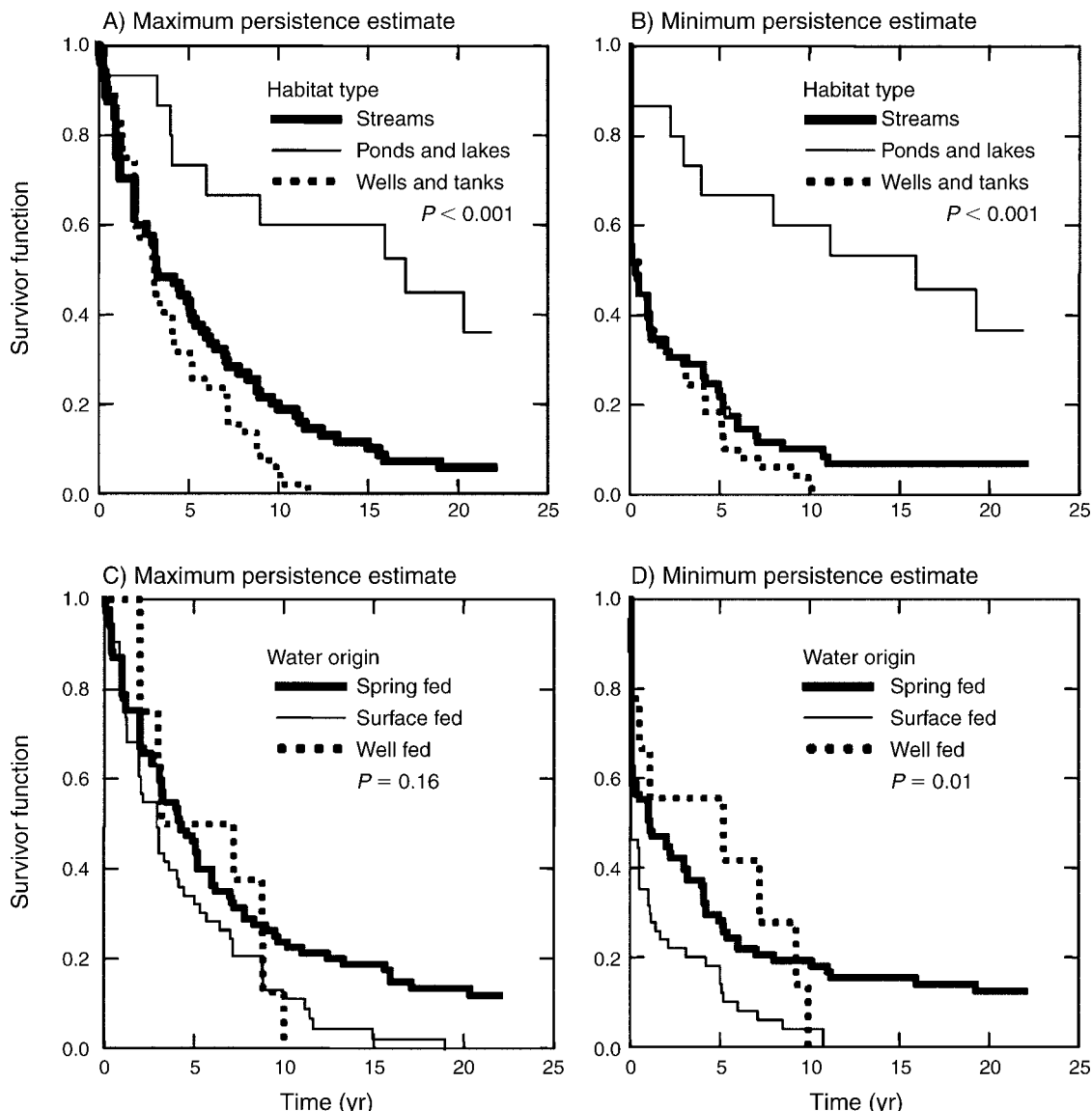


FIG. 5. Survival plots showing how the stratification variables habitat type (A and B) and water source (C and D) influenced maximum and minimum population persistence times for translocated populations of Gila topminnow.

tions ($N = 52$ translocations; $\chi^2 = 13.22$, $df = 2$, $P = 0.001$; Fig. 7C, D).

Lastly, we note that a similar filtering process provides additional insight into the issue of how well populations of Monkey Spring persisted conditional on when they were initiated. In particular, populations stocked with fish from Monkey Spring appeared to suffer persistence problems, regardless of the year period in which they were stocked. For example, of the 17 populations translocated with Monkey Spring stock in 1981 or earlier, only two were still extant in 2003 ($2/17 = 0.118$). During 1982–1983, there were 101 translocations of Monkey Spring fish stockings, of which six were still extant ($6/101 = 0.059$). Of trans-

locations in 1984 and after, 12 stockings occurred, but only one was extant ($1/12 = 0.083$). These results, yielding an overall persistence of $9/130$ (0.070) for Monkey Spring stockings, showed far less success than the $6/12$ (0.5) persistence level of translocations originating from non-Monkey Spring stocks (Yates corrected $\chi^2 = 17.3$, $df = 1$, $P < 0.001$).

DISCUSSION

Survival plots for the overall translocation data set paint a rather grim picture for translocation as a conservation tool for establishing sustainable populations of Gila topminnow (Fig. 3), with 50–70% of translocations failing within the first five years. To

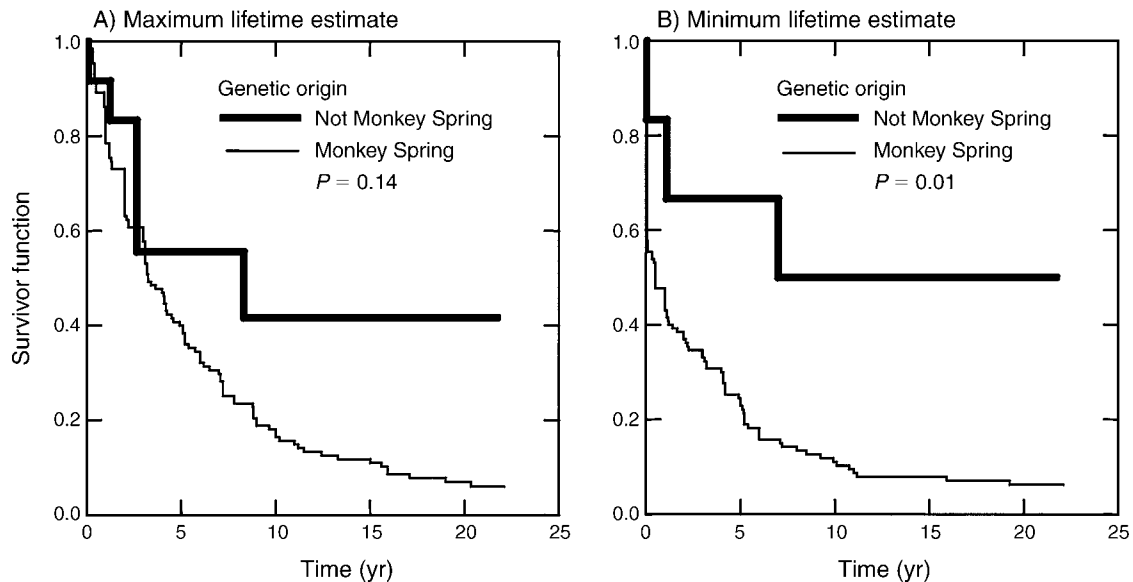


FIG. 6. Survival plots showing how the stratification variable genetic origin influenced (A) maximum and (B) minimum population persistence times for translocated populations of *Gila topminnow*.

improve the success of translocation as a conservation technique, it is essential to identify factors that will lengthen the period of time before restocking is necessary. That issue, analyses of which have implications for other at-risk species, is the focus of the rest of this section.

Our analysis has demonstrated that elements from several classes of factors appear to have influenced the persistence time of translocated populations of *Gila topminnow*. These include (1) details of the translocation activities (i.e., seasonality of translocation), (2) habitat-specific factors (i.e., the habitat type into which the translocation took place), and (3) population-specific factors (i.e., the genetic origin of the fish stocked). We discuss each of these three issues in turn.

Depending on the analysis, translocations stocked in July–December (about half of which occurred in September; Fig. 2B) persisted 3–5 times longer than those stocked in May or June, which together accounted for 64% of translocations (Figs. 4C, D, 7C, D). One possible explanation for this result stems from the idea that *Gila topminnow* lifespan is linked to sexual maturation, which in turn depends on the time of year in which the fish were born (USFWS 1984). Constantz (1974) and Schoenherr (1977) both found that in springs with constant water temperature, individual *Gila topminnows* born in January or February bred by July and died by September, whereas those fish born in summer or fall gave birth in the following spring and died that summer, living approximately one year. In addition, males from Monkey Spring (which was the source of many stockings) have delayed maturation by 13–17 days relative to other *Gila* drainage populations (Cardwell et al. 1998). This delayed maturation may be disadvanta-

geous in sites with a high degree of environmental variation, which is typical of most habitats that received *Gila topminnow* translocations.

If such differences in life span or timing of reproduction and maturation were also associated with differences in mating success, brood size, or offspring quality, they might account for the greatly increased persistence times of populations translocated in the period July–December. The documents available to us did not make clear why so much stocking occurred in May and June. One possibility is that these are some of the hottest months in the Sonoran Desert, and thus sites with water at these times might be expected to retain water through the remainder of the summer. Another possibility is that the intensive fieldwork necessary for translocations is more easily accomplished when summer-only field crews become available, but still before the monsoon season (typically, July–August) makes fieldwork more difficult due to flooding and road problems. Whatever the reason, the available data suggest that populations of *Gila topminnow* translocated in May or June are very unlikely to persist for more than a few years, whereas those translocated at other times of year are likely to fare better.

Another result that may be explained by the life history of *Gila topminnow* is the finding that populations translocated into ponds and lakes persisted significantly longer than populations translocated into either streams or wells and tanks (Figs. 5A, B, 7A, B). These results agree with the documented environmental preferences of *Gila topminnow*, which prefers quiet, warm waters with slow current and abundant aquatic vegetation (Minckley 1999). Such habitats mimic (in a simplified manner) the backwaters, cutoff channels, and

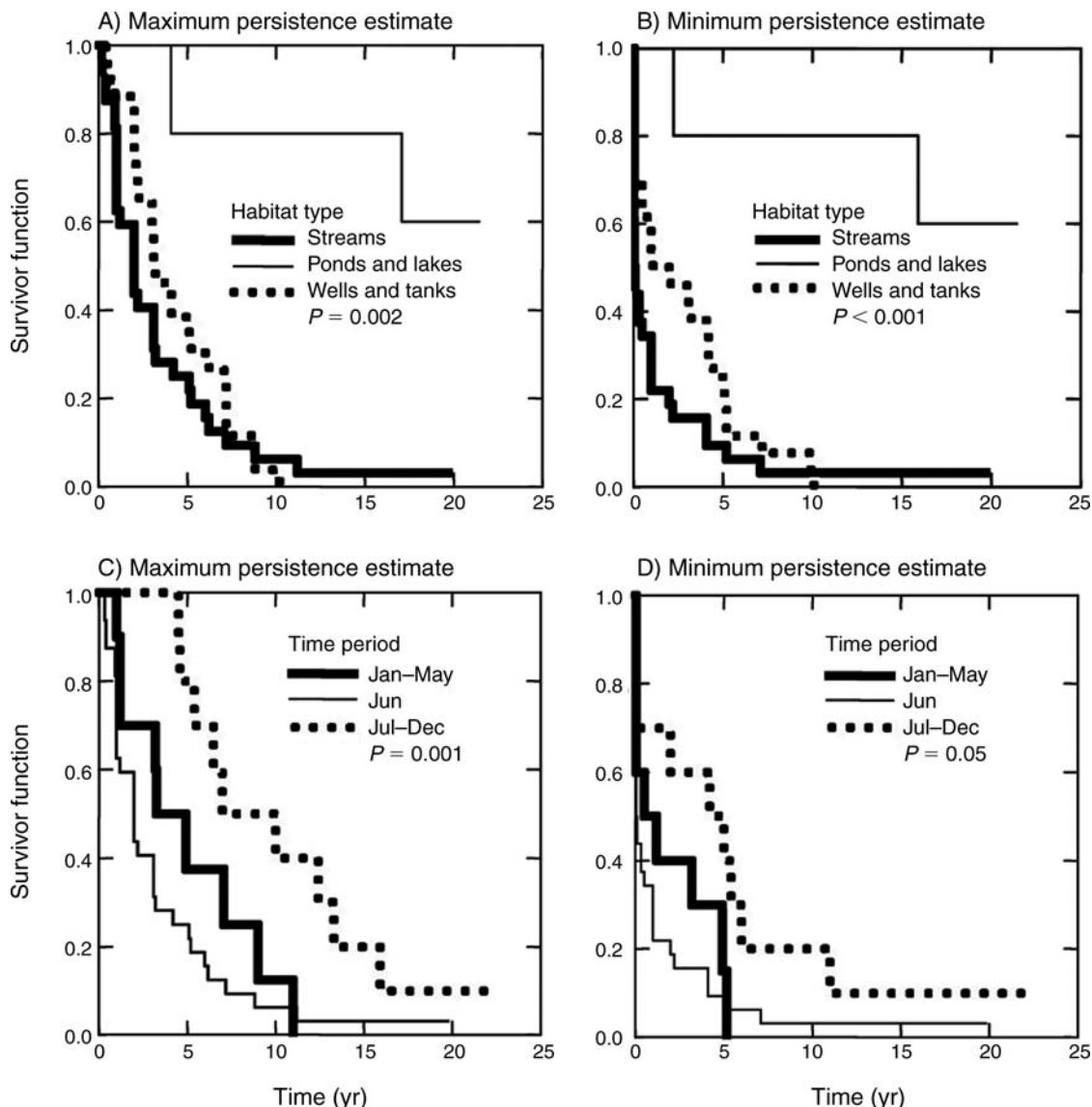


FIG. 7. Survival analyses on “filtered” subsets of the Gila topminnow translocation database. (A, B) Effect of stratification by habitat type for those translocations stocked during June with fish originating from Monkey Spring. (C, D) Effect of stratification by time period (season) for translocations stocked into streams with fish originating from Monkey Spring.

cienea trench pools of (now rare) natural Gila topminnow habitats.

Much of the recent scientific research regarding the Gila topminnow has focused on the characterization of its genetic diversity across the four geographically distinct areas that include all extant natural populations. These regions include Cienega Creek drainage, Sonoita Creek drainage, upper Santa Cruz River drainage, and the Bylas (Gila River) area (Sheffer et al. 1997). Further work on populations within these regions recommended that two evolutionarily significant units (ESU) and four management units (MU) be recognized (Hedrick et al. 2001). These included Monkey Spring and Cottonwood Spring in one ESU, with the remaining populations

being included in a second ESU that was subdivided into four MU based on the four regions. When originally approved, the recovery plan for Gila topminnow provided that downlisting of the Gila topminnow would be achieved once “...Twenty populations have been successfully reestablished in the wild, within historic range, and have survived for at least three years” (USFWS 1984), but the genetic origin of these populations was not considered in this original plan. As a result, all but two translocations before 1986 were made with fish originating from Monkey Spring (Simons et al. 1989). In laboratory studies, Quattro and Vrijenhoek (1989) demonstrated that fish from two of the geographically distinct populations (Monkey Spring and

Sharp Spring) differed in four correlates of fitness (survival, growth, early fecundity, and developmental stability). Fish from Monkey Spring lacked allozyme variation and displayed the lowest fitness in all four traits, whereas fish from Sharp Spring had higher heterozygosity and fitness (Quattro and Vrijenhoek 1989). Because of those findings, translocations after 1984 generally used Gila topminnows originating from Sharp Spring (Sheffer et al. 1997). The results of Quattro and Vrijenhoek (1989) were disputed by Sheffer et al. (1997), who found no relationship between heterozygosity and fitness for populations from the four regions previously listed. Current recommendations for translocation dictate that all remaining lineages of Gila topminnow be preserved and used for translocations at sites in the same area as their natural source population (Sheffer et al. 1997, Weedman 2000, Voeltz and Bettaso 2003).

Our results (Fig. 6A, B) suggest that populations stocked with fish originating from sources other than Monkey Spring did indeed persist longer than populations stocked with fish from Monkey Spring. Consequently, these findings support the notion that fish originating from Monkey Spring are not the best choice for restocking in the Gila River system at large (Quattro and Vrijenhoek 1989, Sheffer et al. 1997). Despite these concerns about the relative fitness of translocated stocks, the consequences of genetic origin/heterozygosity for population persistence in Gila topminnow have not been fully explored. Indeed, few studies of any species have been able to demonstrate a link between fitness correlates measured in the laboratory and the extinction risk of populations (but see Saccheri et al. 1998).

In contrast to previous analyses of mammalian and avian translocation efforts (Griffith et al. 1989, Wolf et al. 1996), we did not find evidence supporting the conclusion that initial population size was a key determinant of population persistence in translocation efforts for Gila topminnow. This result, which also runs counter to expectations based on studies of fish translocations (Hendrickson and Brooks 1991), may perhaps be explained by the life history of the Gila topminnow. This species possesses several life history traits that would seem to facilitate rapid population growth. In particular, the Gila topminnow can reproduce throughout the year, exhibit superfetation, produce large broods (in comparison with other livebearers), and has a relatively short gestation period of 24–28 days (Minckley 1999).

Based on our analyses, an “ideal” translocation effort, one that maximizes persistence time for a translocated Gila topminnow population, is one that occurs during the late summer or autumn months, uses fishes originating from a lineage other than Monkey Spring, and occurs into a spring-fed pond or lake. Quantitative recommendations obtained from Brooks (1985) further specify that

the pond ideally should be located at an elevation <1600 m, with an area <2 ha and a depth <2 m.

In addition to this specific set of recommendations, several other interesting results have emerged from the compilation of the Gila topminnow translocation data set. The sporadic monitoring technique, used because constant surveillance of translocated populations is logistically and fiscally impractical, makes quantifying population persistence at best a rough estimation. The technique of assigning both a minimum and maximum persistence estimate adds some biological realism to the population persistence estimate by acknowledging the idea that, under sporadic monitoring, a population often persists longer than the date when it was last observed. Future investigations that quantify population persistence in sporadically monitored systems should consider using both minimum and maximum persistence estimates (or perhaps some combination of the two metrics) to add more biological realism and to document the two discrete time points between which population extinction occurred.

An important caveat to this recommendation is that the adoption of two persistence metrics allows for the possibility of mixed results, such as was the case for our analyses of the effects of water source (Fig. 5C, D) and year of stocking (Fig. 4A, B). In the latter of these cases, at least, the focal treatment may have been confounded with underlying variation in the data set (i.e., the inter-sample interval tended to be longer earlier in the data set). Such complications are a necessary evil of compiled, “opportunistic” data sets like the Gila topminnow database. When it is logistically and ethically possible, one strategy for minimizing such difficulties would be to adopt an “experimental” approach to population translocations in which individual translocations were designed to be “replicates” within an ANOVA-type framework where intersite variation was controlled, as far as possible, to focus on variation in one or a few treatments (e.g., habitat type, time period of stocking). This overly idealistic scenario is probably better suited to experimental releases of biological control agents than to translocations of endangered species. However, for species that breed readily in captivity and for which loss of translocated populations could be more readily tolerated (e.g., populations designated “experimental–nonessential” under the U.S. Endangered Species Act), adopting a controlled, experimental framework to study population persistence would probably provide greater insights than the type of retrospective survival analyses that we performed here.

The estimation of a “false-absence” rate is another novel result emerging from the translocation data set. We attributed to observational error situations in which Gila topminnows were declared to be absent during one visit, but were then found during a following visit. Long-distance dispersal from other translocation sites is very unlikely, given the highly fragmented nature of the

habitats; however, short-distance dispersal from nearby unknown or unsurveyed aquatic habitats seems possible for at least a few of the nine sites with false absences. This quantified false-absence rate of 6% provides insight into the presence of error in a data set based on observational information that may prove useful for managers. The implication is that, with few exceptions, when Gila topminnows are deemed absent from a site, they really are absent.

The Gila topminnow was one of the first species to be listed as endangered in the United States and also was among the earliest to have a completed recovery plan. As should be expected with any such "firsts," the conservation history of the Gila topminnow has been somewhat problematic and illustrates deficiencies in our understanding of endangered species management (Simons et al. 1989). Nonetheless, it also presents opportunities for retrospection that can inform future efforts and that have relevance beyond this one species. The plethora of translocation data available for Gila topminnow has allowed us to examine what has worked and what has not worked in efforts to develop self-sustaining populations of the species. Our approaches, such as the use of both minimum and maximum persistence estimates and the estimation of a false-absence rate in observational data sets, are advantageous in that they provide increased biological realism to the analyses and help us to understand how much confidence we should have in the data. More broadly, our adoption of survival analysis as our framework for statistical analyses would appear to have wide utility in the study of translocation efforts, releases of biological control agents, or even metapopulation studies. Because no population, whether it be natural or translocated, can be expected to persist forever, what becomes important is an understanding of the factors that promote long-term population persistence and those that promote early collapse. When coupled with solid monitoring data, a survival analysis framework affords such insights.

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APPENDIX

Database of well-documented translocations of Gila topminnow for analysis of translocation success (*Ecological Archives* A016-058-A1).