



# Management of interactions between endangered species using habitat restoration

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## ABSTRACT

Commonly used conservation strategies may be insufficient when deleterious interactions between co-habiting endemic species occur. The decline in the population size of the endangered Leon Springs pupfish, *Cyprinodon bovinus*, in Diamond Y Spring, Texas has been partially attributed to egg-predation by the endangered Pecos gambusia, *Gambusia nobilis*. This interaction is related to changes in habitat availability; therefore, we aim to manage the conflict via restoration of the breeding habitat. We hypothesized that altering the habitat to expand shallow breeding areas would result in a decrease in the number of gambusia preying on the eggs of spawning pupfish pairs and an increase in the number of males defending territories. In 2 years following the habitat modification, we observed resurgence in the pupfish breeding population and a decrease in egg-predation pressure around spawning pupfish pairs. Additionally, after altering the habitat, gambusia were more dispersed throughout the habitat, as the low numbers of gambusia in a territory were stable regardless of spawning or aggressive behaviors by pupfish. To our knowledge, this is the first empirical example of effective management of deleterious interactions between two endangered species by means of habitat restoration.

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## 1. Introduction

Conservationists view many desert springs as refugia because of their small size, their apparent isolation, the uniqueness of their aquatic fauna, and that they are considered to be the remnants of much larger bodies of water that existed thousands of years ago (Hubbs and Miller, 1948; reviews in Hocutt and Wiley, 1968; Echelle et al., 2005; Shepard, 1993). The increasingly common strategy of conserving species via protection of the entire habitat or ecosystem (reviewed in Hoekstra et al., 2002; Likens et al., 2009) has been implemented to conserve many desert springs throughout the southwestern United States (reviewed in Kodric-Brown and Brown, 2007). Habitat based approaches to protect small refugia have focused largely on limiting human access and using legal means to prevent water loss through agriculture (Saunders et al., 2002; see Martin and Wilcox, 2004). For example, in 1984 the Ash Meadows National Wildlife Refuge was created to assist in the broad conservation of multiple desert springs and their endangered inhabitants (reviewed in Kodric-Brown and

Brown, 2007). However, “natural” ecological changes have occurred in some springs that have appeared to threaten the breeding areas of fishes. In the Ash Meadows refuge, limited access of humans and livestock to the springs led to increases in vegetation, reducing aquatic habitats and fish populations (Kennedy et al., 2005; Kodric-Brown and Brown, 2007). While interventions have occurred, these have had limited success (Echelle et al., 2001; Kennedy et al., 2005; see also Kodric-Brown and Brown, 2007).

In addition to protecting the refugia as a whole, conservation efforts in desert springs have focused on direct preservation of particular species. One such group of fishes, the pupfishes (*Cyprinodon* sp.), are highly endangered, largely because each species is usually restricted to one or two desert springs. Actions associated with the implementation of single species management of pupfishes have had mixed results. Long-term demographic and genetic monitoring has identified species in peril and restoration efforts have reestablished some species (e.g. Echelle et al., 2004). Other efforts have been less successful. For example, Minckley (1995) suggested that endangered species, such as pupfishes, should be transplanted to artificial (e.g., fish hatchery pools) or semi-artificial (reservoirs, golf ponds) areas. However, Wilcox and Martin (2006) observed that both genetic and phenotypic characters change once pupfish are bred in unnatural environments (see also Collyer et al., 2005; Koike et al., 2008).

Conservation strategies focused on single species and those based on multiple species or ecosystem approaches each have

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advantages and limitations. Recovery plans focusing on a single-species may be more effective (Boersma et al., 2001), however, only a small fraction of species can be targeted for conservation using this approach due to limited time, financial and scientific resources. Further, some resources, such as knowledge about rare species, may be too limited to contribute to effective management actions (Tear et al., 1995). Additionally, species-specific plans may result in recommended management actions that are in opposition to each other (LaRoe, 1993; Thirgood et al., 2000; Barrows et al., 2005). Advantages of multi-species recovery plans include increased efficiency of conservation resources, wider coverage of biodiversity and decreased conflicts in conservation planning (Grumbine, 1994; Brunner and Clark, 1997; Jewell, 2000). However, multi-species recovery plans may overlook important aspects of target species biology (Clark and Harvey, 2002) and are less effective than single species approaches (Boersma et al., 2001) while broad scale protection of habitats or ecosystems may unintentionally provide protection for invasive species. Given the diversity of conservation strategies, the most appropriate strategy may be difficult to identify and implement. Additionally, any conservation strategy may be insufficient if it does not consider ongoing changes in habitats and associated changes in species requirements.

Neither the single-species nor ecosystem based conservation strategies directly address the potential for deleterious interactions between co-habiting endemic species. Strategies to conserve species involved in such conflicts are still being formalized and have rarely been implemented (Bascompte and Stouffer, 2009; Tylanakis et al., 2010). These relationships are rare, but may occur when species compete with each other for resources (e.g. seabirds, Oro et al., 2009) and will become increasingly common with increased limitations on habitats and resources (Soulé et al., 2003; Tylanakis et al., 2008). This type of interaction has been described for the endangered Leon Spring pupfish (*Cyprinodon bovinus*) and the endangered Pecos gambusia (*Gambusia nobilis*). Gumm et al. (2008) observed that, in the summer of 2006, only one territorial male *C. bovinus* remained in a spring that held over 50 territorial males in 1998 (Leiser and Itzkowitz, 2003). The initial loss of about half of the pupfish territories occurred after emergent plants, such as bulrush (*Scirpus robustus*), eliminated large portions of the pupfish's spawning areas (pers obs). Gumm et al. (2008) suggested that the remaining decline was not caused by further habitat loss but by egg predation by the gambusia, similar to the effects invasive gambusia have on other pupfish (Rogowski and Stockwell, 2006). Prior to the loss of shallow breeding areas, gambusia were spread through most territories making their impact on spawning pairs seemingly negligible (Leiser and Itzkowitz, 2003). Increased habitat limitations, however, may have funneled the gambusia into the remaining shallow areas used for spawning by the pupfish. Given that both species are endangered, any attempt to reduce the negative interactions on pupfish by gambusia must be made without any deleterious consequences for the gambusia.

Our objective was to manage the interaction between pupfish and gambusia, in order to increase the pupfish population without deleterious consequences to the gambusia. Additionally, we aimed to examine the relationship between habitat availability and egg predation by gambusia. Based upon the observations and conclusions of Gumm et al. (2008) and previous restoration and theoretical efforts (Watters et al., 2003; Kennedy et al., 2005), we predicted that expanding the available breeding habitat of the pupfish would produce two results: first, that the number of gambusia preying on the eggs of spawning pupfish pairs would decrease and, second, that the number of male pupfish defending territories would increase (Watters et al., 2003). Gumm et al. (2008) reported densities of gambusia near spawning pairs about five times higher

than densities reported at non-spawning locations; it was presumed that this difference was caused by locally dispersed gambusia quickly swimming to, and aggregating around, spawning pupfish pairs. If gambusia passively accumulate within pupfish territories, we hypothesized that changes in gambusia aggregation around spawning pupfish may be due to changes in local dispersion patterns among gambusia. Consequently, we predicted that if the numbers of gambusia around pupfish pairs declines with the expansion of the breeding habitat, the density of gambusia in the territories in the absence of pupfish spawning should show a proportional decline as well.

## 2. Methods

### 2.1. Study system

The Leon Springs Pupfish, *C. bovinus*, occurs in several springs located approximately 15 km north of Ft. Stockton, Texas. The largest pool located at the headwaters, Diamond Y Spring, has been intensively studied since 1997. In the breeding season from April to October, *C. bovinus* males establish small territories, defending the hard substrate in shallow depths that are typically less than 15 cm. Pupfish species are promiscuous, with females entering territories, laying one to several eggs and then either moving to a different territory to continue spawning or leaving the breeding grounds for deeper water. Leiser and Itzkowitz (2003) described the social system in which there are three male alternative reproductive tactics consisting of large territorial males, medium-sized satellite males and small sneaker males. Both satellite and sneaker males will spawn with females irrespective of location within the territory and are, on the whole, reproductively less successful than males expressing the territorial tactic. When large territorial males are numerous, they hold tightly clustered, small territories (approximately 30 cm in diameter) and rigorously defend their borders against other territorial males and non-territorial intruders. Males of medium size, typically express satellite behaviors but can hold territories when large males are not present (*C. bovinus*, M.I. pers obs; *C. elegans*, Leiser and Itzkowitz, 2002, 2003).

We recorded the number of territorial pupfish every June from 2001 to 2009. The number of territorial males serves as an estimate of population size. Territories have been observed only in a small section of the Diamond Y Spring, and breeding has never been recorded anywhere else in the spring. Considering the importance of the territorial males to the pupfish mating system and resulting propagation, the number of territorial males may serve as an indicator of population demographics. While the spring is approximately 419 m<sup>2</sup>, breeding is currently limited to an 8 m<sup>2</sup> area. Additional shallow areas are covered with soft flocculent substrata or, more typically, populated with dense emergent vegetation. In 1998, the breeding area was larger, and supported approximately 50 territories. Beginning in 2000, for unknown reasons, approximately half of the available breeding area was filled in with emergent plants (i.e., *Scirpus*) and there was a decline to fewer than 20 territories over 2 years. The remaining open shallow area was termed the 'natural shelf'. Although the natural shelf habitat appeared to remain unchanged, in 2006 only one territorial male and several non-territorial (satellite) males were observed (see Gumm et al., 2008). In January 2007, we attempted to restore the initial breeding habitat by removing the roots of the emergent vegetation. To prevent regrowth, we covered the bottom with cement tiles (30.5 cm × 20.3 cm × 5.1 cm). Cement substrates are commonly used in refugia and hatchery breeding populations and pupfish readily spawn on this hard, porous surface (J.M.G., pers obs). The resulting open area added approximately 4 m<sup>2</sup> of shallow habitat to the already available natural shelf.

## 2.2. Assessment of species interactions

Estimates of gambusia density within pupfish territories are not straightforward because they are directly related to the ability of the territorial pupfish to exclude the gambusia. For this reason we used two estimates: (1) the number of chases directed by the pupfish male toward the gambusia within his territory and (2) the number of gambusia found near a stationary tag placed within the territory. To label the location of territorial males, we placed numbered white plastic tags (2 cm × 5 cm) throughout the shallow areas. From 2001 to 2009, we video recorded each territorial male for 20 min, with at least one white tag within view of the male. Each territorial male was recorded between 2 and 5 times each summer and male behavior was assessed, including the number of chases toward gambusia and the number of spawns by the territorial male. Multiple observations were averaged to generate a robust estimate of male behavior. The number of chases directed toward gambusia by territorial pupfish males was also analyzed across all 9 years of the study (2001–2009, excluding 2006 due to a lone territorial male) using an ANOVA and subsequent Newman Keuls tests.

To examine whether the habitat manipulation influenced the number of gambusia preying on freshly laid pupfish eggs, we used the methods described in Gumm et al. (2008). Briefly, during the summers of 2006 and 2008, we photographed pupfish pairs that were spawning and later counted the number of gambusia within 5 cm (approx. one body length) of the pair. At irregular intervals, we also photographed the white tags and counted the number of gambusia within 5 cm of the tag. The data from 2006 was published in Gumm et al. (2008) and we also use it here to compare with subsequent years. We analyzed data from 2006 and 2008 using a two-factor ANOVA coupled with the Newman Keuls paired comparison test.

In 2009, we altered the sampling regimen to test the hypothesis that the number of gambusia within a territory was significantly correlated to the number of gambusia found near the spawning pupfish male. That is, when a territorial male pupfish was observed spawning, we counted the number of gambusia found within 5 cm of the pupfish pair however, unlike the previous 2 years, we counted the number of gambusia near the tag within this territory during the same observation period (when spawning was not occurring). This modification allowed us to infer gambusia density by correlating the number of gambusia found within a pupfish's territory and the number of gambusia found near the same pupfish male while he spawned using a Pearson Correlation Test. For consistency in our statistics across years, a paired *t*-test was also used to test for differences between gambusia near spawnings and tags in the absence of spawning. In 2009, we were unable to analyze tag data for one territorial male reducing the sample size from 9 to 8 males.

We cannot directly compare the relationship between the numbers of gambusia near tags and numbers of gambusia near spawning pupfish pairs across all years as this relationship is confounded by the different sampling regimes between 2006/2008 and 2009. To disentangle this relationship, we used separate ANOVAs and Newman Keuls tests to compare the gambusia numbers near tags and the number of gambusia near spawning pupfish pairs independently across the 3 years (2006, 2008 and 2009). Treating gambusia numbers near tags and gambusia numbers near spawning pupfish pairs separately removed the relationship between tag data and spawning data and allowed for comparison across years. Due to the use of multiple statistical tests, a Bonferroni Correction results in the significance level being set at  $p < 0.0125$ .

## 3. Results

### 3.1. Pupfish population recovery

In the three summers after the emergent plants were removed, the total number of territories held by large pupfish males ranged from 5 to 11 and this range was similar to that observed prior to the decline in 2006 (Fig. 1). However, the distribution of the territories located in shallow depths of the spring changed. While all territories were found only on the 'natural shelf' prior to the vegetation removal, in subsequent years they were widely distributed across both the natural shelf and the newly exposed areas.

### 3.2. Effects of habitat modification on gambusia

As a result of the habitat modification, the abundance of gambusia near breeding pupfish declined. When comparing 2006 and 2008, the number of gambusia found near spawning pupfish pairs and near tags with no spawning occurring was significantly different (ANOVA,  $F_{3,254} = 110.5$ ,  $p < 0.00001$ ; Fig. 2). There were significantly more gambusia near spawning pupfish pairs than near tags in 2006 (Newman Keuls test,  $p < 0.00001$ ) but not in 2008 (NK test,  $p = 0.49$ ). There were significantly more gambusia near spawning pupfish in 2006 than 2008 (NK test,  $p < 0.00001$ ) but there was not a significant difference in the number near tags (NK test,  $p = 0.89$ ). Considering only 2009, there were significantly more gambusia near a spawning territorial pupfish than near the tag within his territory when he was not spawning (Paired *t*-test,  $t = 9.66$ , d.f. = 99,  $p < 0.00001$ ; Fig. 2).

Across the 3 years there was a significant decline in the number of gambusia near tags (ANOVA,  $F_{2,201} = 18.5$ ,  $p < 0.00001$ ). Significantly more gambusia were found near tags in 2006 than in 2008 or 2009 (NK test  $p < 0.001$ ,  $p < 0.00003$ , respectively) and 2008 was not significantly different from 2009 (NK test  $p = 0.02$ ), although there was a strong declining trend. There was also a significant difference in the number of gambusia near spawning pairs across the 3 years (ANOVA,  $F_{2,251} = 146.4$ ,  $p < 0.000001$ ). Significantly more gambusia were found near pairs in 2006 than in 2008 and 2009 (NK test  $p < 0.00001$ ,  $p < 0.00001$ , respectively) but 2008 was not significantly different from 2009 (NK test  $p = 0.21$ ).

Excluding the year 2006 when only one pupfish held a territory, there was an overall significant difference in the number of chases

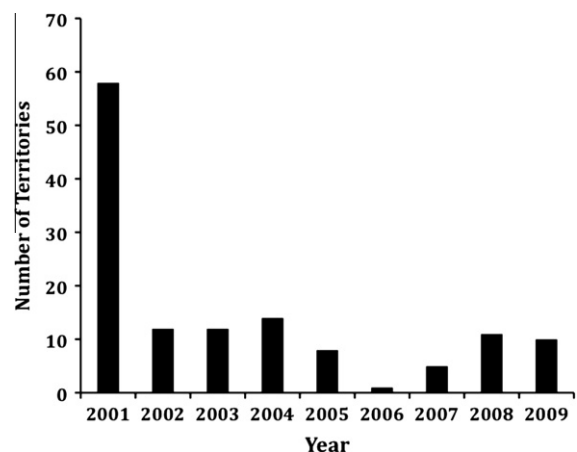
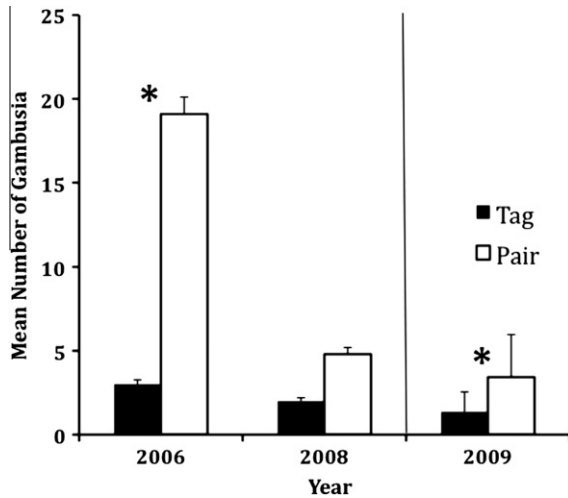


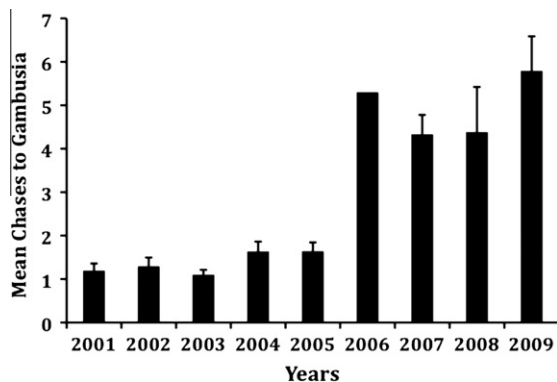
Fig. 1. The number of pupfish breeding territories observed in Diamond Y Spring, Texas. From 2001 to 2006, territories occurred only on the "natural shelf." In subsequent years, territories were observed on both the natural shelf and the areas exposed by the habitat restoration.



**Fig. 2.** The mean number ( $\pm$ SE) of gambusia within one body length (5 cm) of tags (black bar) or spawning pairs (white bar). Asterisks indicates significance levels in which  $p < 0.05$ . The data for 2006 was taken from Gumm et al. (2008). See text for additional details.

directed toward gambusia across years (ANOVA,  $F_{7,85} = 17.96$ ,  $p < 0.00001$ ; Fig. 3). The number of chases directed at gambusia from 2001 to 2005 was not significantly different from each other (NK test,  $p > 0.05$ ) nor were there significant differences among years 2007–2009 (NK test,  $p > 0.05$ ). However, there were significantly more chases in 2007–2009 than in previous years, 2001–2005 (NK test,  $p < 0.001$ ). In 2006, the mean number of chases directed at gambusia by the single territorial pupfish was similar to the number of chases by territorial pupfish in subsequent years (Fig. 3).

We also considered the number of gambusia found near the tags when the territorial pupfish males were not spawning as an estimate of gambusia densities within territories. Similar to the number of chases, numbers of gambusia at tags were relatively stable from 2006 to 2009 (see above). In 2009, there was a significant positive correlation between the mean number of gambusia around a tag within the territory of a pupfish and the mean number of gambusia around the same male when he spawned ( $n = 8$ ,  $r = 0.94$ ,  $p < 0.0001$ ). However, chasing was not significantly correlated with mean number of gambusia near tags ( $n = 8$ ,  $r = -0.37$ ;  $p = 0.33$ ), or with the mean number of gambusia near spawning pairs ( $n = 8$ ,  $r = -0.27$ ,  $p = 0.48$ ).



**Fig. 3.** Mean (SE) mean number of chases toward gambusia for all territorial males in each year. See Fig. 1 for sample sizes. No SE was calculated for 2006 because there was only one territorial male.

#### 4. Discussion

The intent of this study was to use habitat modification to manage the deleterious interaction between two endangered species. Specifically, we tested the prediction that managing egg predation by gambusia would allow for recovery of the pupfish population. Our hypothesis that expanding the pupfish spawning habitat would reduce deleterious interactions was supported. Additionally, after expanding the shallow areas, there was a corresponding increase in the number of territorial male pupfish over the next 2 years (2008 and 2009; Fig. 1). Increasing the available breeding area is predicted to cause a direct increase in the number of territorial males (Kodric-Brown, 1978). Specifically, the ‘phenotype management’ hypothesis predicts that increasing breeding areas results in non-territorial males switching to the territorial tactic (Watters et al., 2003). Stemming from this prediction, we would expect a corresponding decrease in the number of non-territorial males if the increase in territorial males was simply due to non-territorial males switching tactics. While we did not quantify the number of non-territorial males, after habitat modification, non-territorial males were still present in the population. Further, in laboratory and field settings, intermediate-sized males defend territories and small males will defend territories in lab settings (*C. bovinus*, M.I. pers obs; *C. elegans*, Leiser and Itzkowitz, 2002, 2003), suggesting that they could have adopted the territorial tactic given the additional available breeding habitat. Thus, removing spatial limitations in breeding areas likely influenced the increase in territorial pupfish, but our findings suggest that other factors also influence the relationship between breeding area, male number and male tactic.

The hypothesis that habitat limitation led to higher numbers of gambusia near spawning pupfish pairs was also supported; there were significantly fewer gambusia observed near pupfish pairs after expanding the habitat (in 2008 and 2009) than when habitat was limited (in 2006; Fig. 2). There were also significantly fewer gambusia around haphazardly placed tags, suggesting that the overall density of gambusia in these areas had declined as well. However, the relative number of gambusia at spawnings and tags differed among years. Compared to the number of gambusia near spawning pupfish pairs, there were about 5-fold fewer gambusia around tags in 2006, while in succeeding years the relative difference between gambusia near spawning pupfish pairs and tags was proportionately much less (Fig. 2). The large numbers of gambusia seen around spawning pupfish in 2006 was unlikely to be due to a uniformly high density on the natural shelf, but rather was caused by a change in behavior in which large numbers of gambusia streamed into the territory when pupfish began spawning. This behavioral clustering and the abundance of gambusia entering territories was not seen in 2008 and 2009. In these later years, spawning pupfish were approached mainly by gambusia already present within the territory. This observation was further supported by data collected in 2009 in which there is a significant positive correlation between the number of gambusia found near spawning pairs and the number of gambusia found within the same territory (i.e., near tags). Taken together, these results suggest that after altering the habitat, gambusia were more dispersed and this resulted in less egg predation around spawning pairs of pupfish.

We also considered the number of chases by territorial pupfish as a potential indicator of the number of gambusia within the territory (Fig. 3). However, there were no significant correlations between the number of chases directed towards gambusia and the number of gambusia recorded near tags or the number of gambusia near spawning pupfish in 2009. These results suggest that differences in the number of gambusia between territories were not a function of male pupfish behavior and further support our



hypothesis that habitat availability influences the distribution of gambusia. The number of chases to gambusia increases, even when the number of gambusia present near spawnings decreases; thus, the dramatic increase in gambusia chases after 2005 may not have been due solely to the influx of gambusia. We suspect that fewer chases towards gambusia prior to 2006 were related to the intense intrasexual interactions between the clustered territorial pupfish. Itzkowitz (1974) observed that the variegated pupfish (*C. variegatus*) preferentially direct their attacks toward conspecific intruders over heterospecific species (e.g., gambusia). The tight clustering of *C. bovinus* territories in 2005 and earlier may have caused males on the natural shelf to divert much of their aggressive behavior toward conspecific neighbors resulting in fewer chases towards gambusia (see Leiser and Itzkowitz, 2003). Neighboring male pupfish frequently disrupted and reduced the spawning success of their neighbors and, therefore, males spent considerable time threatening and attacking their neighbors rather than attacking gambusia.

## 5. Implications and conclusions

Our strategy to conserve *C. bovinus* by expanding open shallow areas is a common practice used in other desert springs (Kodric-Brown and Brown, 2007). In those cases, the disappearance of the habitat had been directly attributed to the decline and often the extinction of the pupfish species. Our observations concur that habitat loss is likely a factor in the severe decline in the *C. bovinus* breeding population. However, the effects of habitat loss were exacerbated by deleterious effects of egg predation by gambusia and as a result, the pupfish breeding population declined more than would have been predicted on the basis of remaining available spawning habitat. We effectively managed the interaction between these two endangered species via restoration of the breeding habitat and observed a corresponding resurgence in the numbers of territorial male pupfish, potentially indicating an increase in population numbers due to the reduction in the number of gambusia that preyed directly on the eggs deposited by spawning pupfish pairs.

Targets of conservation and restoration efforts vary from individual species to entire ecosystems, however these strategies may be insufficient to address interactions between species. Conservation efforts on interacting species typically focus on changes in abundance, distribution and behavior of a species after decline or removal of another (Mills et al., 1993; Soulé et al., 2003). Changes in behavioral dynamics between species may also be detrimental and may lead to species decline (Gumm et al., 2008). Deleterious interactions between endemic, endangered species are rare, but will increase in frequency with increasing pressures on resources (Soulé et al., 2003). This study utilizes one of the first known examples of changing dynamics between endemic, endangered species (Gumm et al., 2008) to manage a conflict between species via habitat modification. While this approach relies upon extensive knowledge of the natural history of target species, it allows for the recovery of a species without negatively influencing another. This study also highlights how knowledge of species behavior can guide conservation efforts. Finally, the indirect nature of this approach may provide an alternative conservation strategy that bridges the gap between species-specific and habitat or ecosystem based conservation strategies.

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## References

- Barrows, C.W., Swartz, M.B., Hodges, W.L., Allen, M.F., Rotenberry, J.T., Li, B., Scott, T.A., Chen, X., 2005. A framework for monitoring multiple-species conservation plans. *Journal of Wildlife Management* 69, 1333–1345.
- Bascompte, J., Stouffer, D.B., 2009. The assembly and disassembly of ecological networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364, 1781–1787.
- Boersma, P.D., Kareiva, P., Fagan, W.F., Clark, J.A., Hoekstra, J.M., 2001. How good are endangered species recovery plans? *BioScience* 51, 643–650.
- Brunner, R.D., Clark, T.W., 1997. A practice-based approach to ecosystem management. *Conservation Biology* 11, 48–58.
- Clark, J.A., Harvey, E., 2002. Assessing multi-species recovery plans under the endangered species act. *Ecological Applications* 12, 655–662.
- Collyer, M.L., Novak, J.M., Stockwell, C.A., 2005. Morphological divergence of native and recently established populations of White Sands pupfish (*Cyprinodon tularosa*). *Copeia* 2005, 1–11.
- Echelle, A.A., Echelle, A.F., Kiner, L., Garrett, G.P., Karges, J., Fishers, W.L., 2001. In: Draw, Diamond Y. (Ed.), Final Report: Monitoring Effects of a Renovation Project on Endangered Fish and Invertebrates. T.P.a.W.D. Endangered Resources Branch.
- Echelle, A.F., Echelle, A.A., Bonnel, L.K., Allen, N.L., Brooks, J.E., Karges, J., 2004. Effects of a restoration effort on an endangered pupfish (*Cyprinodon bovinus*) after genetic introgression by a non-native species. In: Loranço-V, M.D.L., Contreras-B, A.J. (Eds.), Homenaje al Doctor Andres Resendez Medina. Universidad Autonoma de Nuevo Leon, Monterrey, Mexico, pp. 129–139.
- Echelle, A.A., Carson, E.W., Echelle, A.F., Van Den Bussche, R.A., Dowling, T.E., Meyer, A., 2005. Historical biogeography of the new-world pupfish genus *Cyprinodon* (Teleostei: Cyprinodontidae). *Copeia* 2005, 320–339.
- Grumbine, R.E., 1994. What is ecosystem management. *Conservation Biology* 8, 27–38.
- Gumm, J.M., Snekser, J.L., Itzkowitz, M., 2008. Conservation and conflict between endangered desert fishes. *Biology Letters* 4, 655–658.
- Hocutt, C.H., Wiley, E.O., 1968. *The Zoogeography of North American Freshwater Fishes*. John Wiley & Sons, New York.
- Hoekstra, J.M., Clark, J.A., Fagan, W.F., Boersma, P.D., 2002. A comprehensive review of endangered species act recovery plans. *Ecological Applications* 12, 630–640.
- Hubbs, C.L., Miller, R.R., 1948. The Great Basin, with emphasis on glacial and postglacial times. II. The zoological evidence. *Bulletin of the University of Utah* 38 *Biological Series* 10, 17–166.
- Itzkowitz, M., 1974. The effects of other fish on the reproductive behaviour of the male variegated pupfish, *Cyprinodon variegatus* (Pisces: Cyprinodontidae). *Behaviour* 48, 1–22.
- Jewell, S., 2000. Multi-species recovery plans. *Endangered Species Bulletin* 25, 30–31.
- Kennedy, T.A., Finlay, J.C., Hobbie, S.E., 2005. Eradication of invasive *Tamarix ramosissima* along a desert stream increases native fish density. *Ecological Applications* 15, 2072–2083.
- Kodric-Brown, A., 1978. Establishment and defense of breeding territories in a pupfish (Cyprinodontidae: Cyprinodon). *Animal Behaviour* 26, 818–834.
- Kodric-Brown, A., Brown, J.H., 2007. Native fishes, exotic mammals, and the conservation of desert springs. *Frontiers in Ecology and the Environment* 5, 549–553.
- Koike, H., Echelle, A.A., Loftis, D., Van Den Bussche, R.A., 2008. Microsatellite DNA analysis of success in conserving genetic diversity after 33 years of refuge management for the desert pupfish complex. *Animal Conservation* 11, 321–329.
- LaRoe, E.T., 1993. Implementation of an ecosystem approach to endangered species conservation. *Endangered Species UPDATE* 10, 3–6.
- Leiser, J.K., Itzkowitz, M., 2002. The relative costs and benefits of territorial defense and the two conditional male mating tactics in the Comanche Springs pupfish (*Cyprinodon elegans*). *Acta Ethologica* 5, 65–72.
- Leiser, J.K., Itzkowitz, M., 2003. The costs and benefits of territorial neighbours in a Texas pupfish (*Cyprinodon bovinus*). *Behaviour* 140, 97–112.
- Likens, G.E., Walker, K.F., Davies, P.E., Brookes, J., Olley, J., Young, W.J., Thoms, M.C., Lake, P.S., Gawne, B., Davis, J., Arthington, A.H., Thompson, R., Oliver, R.L., 2009. Ecosystem science: toward a new paradigm for managing Australia's inland aquatic ecosystems. *Marine and Freshwater Research* 60, 271–279.
- Martin, A.P., Wilcox, J.L., 2004. Evolutionary history of Ash Meadows pupfish (genus *Cyprinodon*) populations inferred using microsatellite markers. *Conservation Genetics* 5, 769–782.
- Mills, L.S., Soule, M.E., Doak, D.F., 1993. The keystone- species concept in ecology and conservation. *BioScience* 43, 219–225.
- Minckley, W.L., 1995. Translocation as a tool for conserving imperiled fishes: Experiences in western United States. *Biological Conservation* 72, 297–309.
- Oro, D., Pérez-Rodríguez, A., Martínez-Vilalta, A., Bertolero, A., Vidal, F., Genovart, M., 2009. Interference competition in a threatened seabird community: a paradox for a successful conservation. *Biological Conservation* 142, 1830–1835.
- Rogowski, D.L., Stockwell, C.A., 2006. Assessment of the potential impacts of exotic species on populations of white sands pupfish *Cyprinodon tularosa*. *Biological Invasions* 18, 79–87.

- Saunders, D.L., Meeuwig, J.J., Vincent, A.C.J., 2002. Freshwater Protected Areas: Strategies for Conservation. *Áreas Protegidas de Agua Dulce: Estrategias para la Conservación*. *Conservation Biology* 16, 30–41.
- Shepard, W.D., 1993. Desert springs—both rare and endangered. *Aquatic Conservation: Marine and Freshwater Ecosystems* 3, 351–359.
- Soulé, M.E., Estes, J.A., Berger, J., Martinez Del Rio, C., 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* 17, 1238–1250.
- Tear, T.H., Scott, J.M., Hayward, P.H., Griffith, B., 1995. Recovery plans and the endangered species act: are criticisms supported by data? *Conservation Biology* 9, 182–192.
- Thirgood, S., Redpath, S., Newton, I., Hudson, P., 2000. Raptors and red grouse: conservation conflicts and management solutions. *Conservation Biology* 14, 95–104.
- Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11, 1363.
- Tylianakis, J.M., LalibertÉ, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biological Conservation* 143, 2270–2279.
- Watters, J.V., Lema, S.C., Nevitt, G.A., 2003. Phenotype management: a new approach to habitat restoration. *Biological Conservation* 112, 435–445.
- Wilcox, J.L., Martin, A.P., 2006. The devil's in the details: genetic and phenotypic divergence between artificial and native populations of the endangered pupfish (*Cyprinodon diabolis*). *Animal Conservation* 9, 316–321.