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Conservation and conflict between endangered desert fishes

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Conservation of naturally sympatric endangered species requires unique considerations. While impacts of invasive species garner much attention, interactions between endangered species must also be managed. The endangered Leon Springs pupfish, *Cyprinodon bovinus*, has suffered a population decline due to decreasing natural habitat. As breeding habitat is lost, *C. bovinus* is also adversely affected by the sympatric, endangered Pecos gambusia, *Gambusia nobilis*. Here, we document interactions between these species, finding significantly more *G. nobilis* accumulated at pupfish spawning events than randomly distributed on breeding grounds in the absence of spawning. As a known egg predator, our results suggest that *G. nobilis* presence at spawnings may further decrease pupfish numbers while also altering the evolutionary dynamics of *C. bovinus* breeding tactics. Habitat restoration may decrease *Gambusia* concentrations or influence *C. bovinus* breeding behaviour and increase the number of territorial males resulting in viable population sizes for both critically endangered fishes.

Keywords: *Cyprinodon*; *Gambusia*; predation; species interactions

1. INTRODUCTION

Direct conflicts between naturally sympatric endangered species present unique challenges to conservation. Antagonism between species may increase as resources, such as food or breeding habitat, become more limited (Barrows *et al.* 2005) and may ultimately result in species loss (Scott & Helfman 2001). Solutions to conflicts between endangered species are difficult to mediate as management typically focuses on individual species and recovery plans can directly oppose one another (Thirgood *et al.* 2000; Barrows *et al.* 2005; Soulé *et al.* 2005). Managing the impacts of invasive species, however, receives much attention and the effects of invasive species on natural populations may provide clues to interactions between historically sympatric species, which must also be addressed and managed (Mooney & Cleland 2001; Soulé *et al.* 2003).

Endangered pupfishes (*Cyprinodon* spp.) endemic to desert spring systems are at risk due to limited habitat availability. Additionally, multiple invasive species have expedited decreases in pupfish frequencies. In a

Cyprinodon species flock in Laguna Chichancanab, Yucatan, an African cichlid (genus *Oreochromis*) invasion resulted indirectly in pupfish (*Cyprinodon simus*, *Cyprinodon maya*) population declines due to food competition, while *Astyanax* spp. invasion resulted directly in pupfish declines (*Cyprinodon esconditus*, *Cyprinodon labiosus*, *C. maya*, *C. simus*, *Cyprinodon verecundus*) through predation on fry and juveniles (Strecker 2006).

Livebearing fishes (Poeciliidae) are commonly invasive due to high reproductive rates and widespread use for mosquito control (Krumholz 1948). Indirectly, invasive livebearers (*Gambusia affinis*, *Gambusia holbrooki*) have caused declines in endemic species because, as generalists, they out compete native species for resources (Courtenay & Meffe 1989; Mills *et al.* 2004; Rehage *et al.* 2005). Invasive *Poecilia reticulata* also sexually harass endangered heterospecifics (Valero *et al.* 2008). Directly, invasive livebearers often prey upon native species (Meffe 1985). The combined effects of exposure to *G. affinis* result in significantly smaller populations of White Sands pupfish, *Cyprinodon tularosa* (Rogowski & Stockwell 2006). Invasiveness, however, is not required for poeciliids to threaten other species and native *Gambusia* species are often sympatric with endangered pupfishes.

Given the widespread negative effects of *Gambusia*, we aimed to understand how *Gambusia* may influence pupfish reproduction by documenting interactions between two endangered species: the Pecos gambusia, *Gambusia nobilis*, and the Leon Springs pupfish, *Cyprinodon bovinus*. These fishes are naturally sympatric; however, the population of *C. bovinus* has been declining. Changing dynamics within either population may lead to alterations in interactions between the species. First, we estimated breeding male *C. bovinus* numbers over seven years. Second, we examined *G. nobilis* behaviour in relation to *C. bovinus* reproduction. *C. bovinus* males defend territories on a breeding shelf and share costs of defence against *G. nobilis* that potentially eat pupfish eggs and interrupt spawnings by intruding into territories and garnering aggression (Leiser & Itzkowitz 2003). As the number of territorial males declines, however, they may no longer be effective at defending against intruders and consequently suffer increased egg predation or complete spawning failure.

2. MATERIAL AND METHODS

(a) Study system

Cyprinodon bovinus and *G. nobilis* are endemic to Diamond Y Spring and associated watercourses near Fort Stockton, Texas. The headwater pool (14×25×3.5 m³) is the largest and historically most stable population of pupfish, although they may also occur in a smaller, intermittent pool (0.3×0.02 m²) and downstream watercourse (Echelle *et al.* 2004). Immigration between pools is possible, however, they are separated by a 1600 m channel choked with bulrush and immigration between watercourses is unlikely due to 3 km of dry land separating them (Echelle *et al.* 2004). This is the only habitat for *C. bovinus* while *G. nobilis* is found in three other Chihuahuan desert spring systems (Hubbs *et al.* 2002). *C. bovinus* has a promiscuous breeding system and males exhibit alternative reproductive tactics with large males defending territories while smaller males acquire spawnings as non-territorial satellites or sneakers (Leiser & Itzkowitz 2003). In the Diamond Y head pool, males defend territories on a rocky shelf (1×3 m²) which is the only known breeding grounds in the pool and associated outflow stream. Females enter spawning grounds and descend to the substrate, pausing until joined by a male. The male sidles next to a

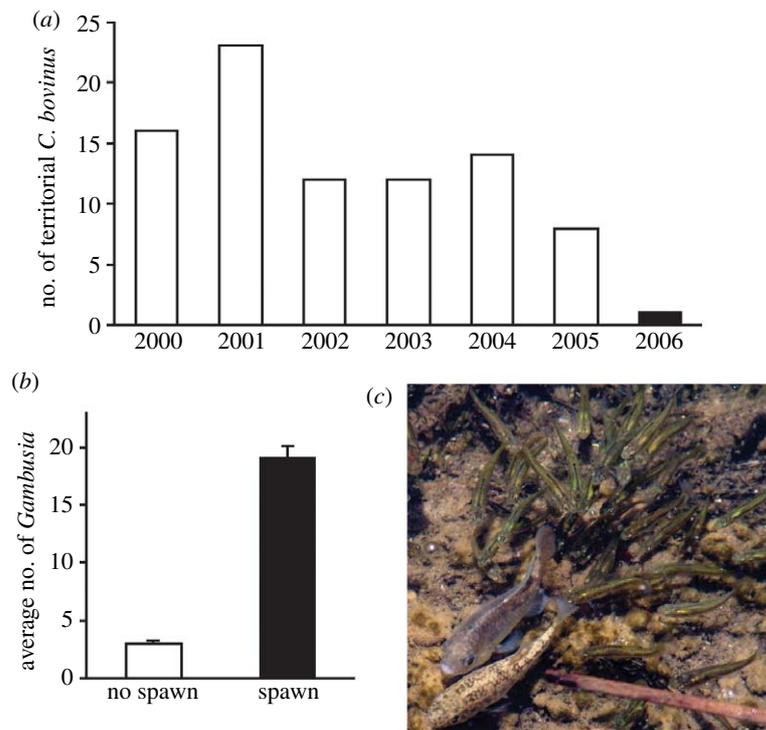


Figure 1. *Cyprinodon bovinus* population size and effects of *G. nobilis*. (a) Population decline of territorial *C. bovinus* males from 2000 to 2006. (b) Mean (+s.e.) *G. nobilis* found in the absence of spawning (white bar) and within one body length of *C. bovinus* spawnings (black bar). (c) Spawning *C. bovinus* attended by an aggregation of *G. nobilis*.

female, performing an S-shaped jerking of the body while the female deposits a single egg on the substratum per spawning.

(b) Population estimate

Pupfish typically breed from April until October. In May and June from 2000 to 2006, we estimated population size by counting territorial males present on the breeding shelf. Between 11.00 and 15.00, videotapes (20 min) were recorded of all areas of the shelf. Tapes were later reviewed to identify all males holding territories.

(c) Species interactions

In 2006, spawning grounds were mapped with weighted tags made of waterproof paper. Tags approximately the length of a large *C. bovinus* ($50 \times 20 \text{ mm}^2$) were placed on the breeding shelf in a grid formation to track the location of territorial males and spawnings. Spawning activity peaks along with daily temperatures, thus observations were conducted from 11.00 to 15.00 between 29 May and 07 June, 2006.

Spawning pairs were identified by following females as they entered the spawning grounds. Digital photographs (Kodak Z740; figure 1c) were taken of spawning pairs immediately after egg deposition. All spawning pairs included in the analysis contained at least one large individual (more than 50 mm). Digital photographs were taken of all tags during intervals between spawning events. Photographs were analysed using KODAK EASYSHARE software. The standard length of the large pupfish or tag was measured on photographs and the number of *G. nobilis* within one body length of the spawning pair or tag was quantified. There was one territorial and an unknown number of satellite males involved in spawnings. The breeding tactic of the spawning male could not be identified in all photographs, but when possible was identified as territorial or satellite based on male size and location on the breeding shelf. Satellite males are smaller in size (Leiser & Itzkowitz 2003) and the territorial male spawned in a restricted area of the shelf with identifiable landmarks. Data were analysed using unpaired *t*-tests with STATVIEW v. 5.0.

3. RESULTS

The number of territorial males in the natural population of *C. bovinus* has declined since 2000 ($r = -0.83$, $p = 0.02$; figure 1a). In 2006, a single territorial male was observed, resulting in a

population size much lower than expected from previous years (95% CI for 2000–2005: 8.84–19.49). This male's territory was similar in size to those held by males in other years (M. Itzkowitz 2000–2006, personal observation).

In 2006, *G. nobilis* were closely associated with pupfish. *Gambusia* descended to the substrate oriented close to the posterior of spawning pupfish pairs and appeared to engage in searching and foraging. Further, *G. nobilis* distribution was based on distribution of spawning pupfish. There were significantly more *G. nobilis* present within one body length of spawnings ($n = 104$) than when no spawning was occurring ($n = 60$; $t(163) = -11.88$, $p < 0.01$; figure 1b). When breeding tactic was identifiable, there were no differences in the number of *G. nobilis* present at spawnings of the territorial male ($n = 35$) compared with satellite males ($n = 24$; $t(58) = -1.83$, $p = 0.07$).

4. DISCUSSION

Territorial male *C. bovinus* have declined since 2000. In other species, absence of territorial individuals results in males abandoning alternative tactics to control available territories (Beletsky & Orians 1987). Smaller male *C. bovinus* can hold territories and, in previous years, have defended low-quality territories, peripheral to the main breeding shelf (Leiser & Itzkowitz 2003). Nonetheless, we observed smaller males expressing satellite behaviour despite the availability of high-quality breeding territories. This may be due to altered costs and benefits of territoriality.

One typical advantage of territoriality in *C. bovinus* is fewer intrusions by *Gambusia* (Leiser & Itzkowitz 2003). In contrast to their observations, we found

high concentrations of *Gambusia* around the one territorial male in our study. This suggests that individual territoriality is not adequate and that a cluster of territorial males is necessary to keep *Gambusia* densities low on spawning grounds. This effect would protect both territorial and satellite males from costs of *Gambusia* including spawning intrusions and egg predation. While we did not test the mechanism by which *G. nobilis* are costly to pupfish, presence of equivalent numbers of *G. nobilis* at the territorial and satellite males' spawnings suggests that the combined costs were similar across mating tactics. The high numbers of *G. nobilis* at spawnings may have resulted in changes in the breeding system such that smaller males remained satellites instead of defending available territories.

Solutions to conflicts in conservation remain inadequate, despite recent emphasis on multispecies and ecosystem-based recovery plans (Barrows *et al.* 2005; Soulé *et al.* 2005). For example, recovery of endangered island foxes (*Urocyon littoralis*) may require the lethal removal of protected golden eagles (*Aquila chrysaetos*; Courchamp *et al.* 2003). In our system, successful removal of *G. nobilis* is impractical; however, if left undisturbed it is likely that *Gambusia* will continue to be favoured at the expense of *C. bovinus*. Long-term management of these species may require multiple approaches, one of which is to manipulate the environment to indirectly solve the conflict between species. For example, artificially increasing the breeding ground area may aid in pupfish recovery via multiple mechanisms. First, by modifying the spatial distribution of resources, males may disperse and escape interrupted spawnings and egg predation associated with high concentrations of *Gambusia*. Habitat restoration may also increase population size by altering the expression of phenotypes via further decreasing competition among males (Watters *et al.* 2003), resulting in more territorial males and increased spawning rates typically associated with high-quality territories.

While the specific environmental changes leading to the decreased numbers of territorial male pupfish are unknown, the altered dynamics between pupfish and *G. nobilis* may indicate an ecosystem at risk. When naturally sympatric species are both endangered, negative interactions must be understood and considered to develop successful recovery plans for all species involved (Barrows *et al.* 2005; Soulé *et al.* 2005). This situation is exemplified by interactions between *C. bovinus* and *G. nobilis*, where the success of one endangered species is ultimately dependent upon management of another endangered species.

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