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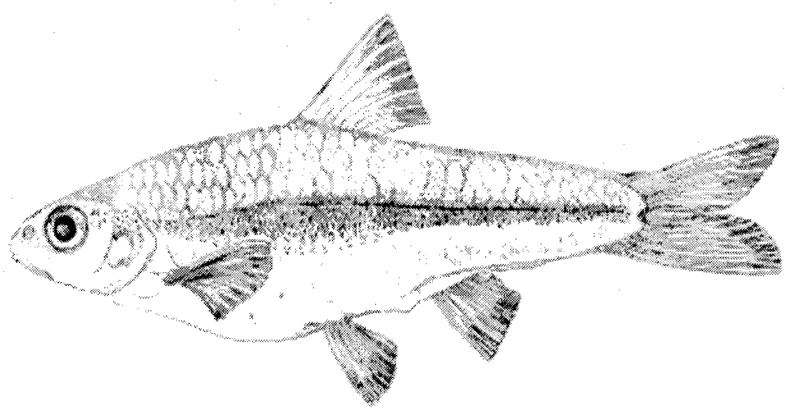

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GARY P. GARRETT AND NATHAN L. ALLAN

Spring-Endemic *Gambusia* of the Chihuahuan Desert

Clark Hubbs

Abstract

Spring endemic fishes are restricted to the vicinity of spring outflows where stenothermal conditions prevail. Stream fishes occupy downstream locations that are substantially more eurythermal. Those circumstances prevail throughout the Chihuahuan Desert where *Gambusia senilis* interacts with *G. hurtadoi* and *G. alvarezi* and *Gambusia affinis* interacts with *G. nobilis* and *G. gaigei*. *Gambusia amistadensis* once occurred in and was restricted to Goodenough Spring where it interacted with *G. affinis* in the Rio Grande. All evidence indicates that similar interactions occur with other fishes, amphipods, crayfish, and salamanders.

Introduction

The fishes of the Chihuahuan Desert require adequate quantity and quality of water. In as much as few lakes occur there, the need is for lentic environments. Throughout most of the southwest United States and northwest Mexico, human desires often negatively impact stream flows. Problems associated with all the fishes can be illustrated by problems with members of the genus *Gambusia*. Many of the fishes are spring endemics that require natural spring flow volumes (Hubbs, 1996, 2001). Often the problem is intrageneric. For example, *Gambusia senilis* and the *affinis* species group are stream fishes and *G. nobilis*, *G. gaigei*, *G. hurtadoi*, and *G. alvarezi* are spring endemics. When spring flow volumes decrease, the stream species gain area at the expense of the spring endemics. Stream species have a competitive advantage away from springs and spring species have a competitive advantage in springs. The primary driving factor is stenothermal vs. eurythermal conditions. Similar interactions occur within cyprinids, centrarchids, and percids in the Chihuahuan Desert. Likewise in Nevada *Crenichthys* is adapted to stenothermal, warm, low dissolved oxygen springs and many native minnows are better as stream fishes. *Crenichthys* can survive in below 0.7 ppm O_2 at 37°C (Sumner and Sargent, 1940; Hubbs and Hettler, 1964). It is unlikely that members of the genus *Cyprinodon* have similar needs for stenothermal water, as *Cyprinodon elegans* populations increased at Phantom Cave Spring when spring flow declined (Hubbs, 2001). Nevertheless, *Cyprinodon* clearly needs adequate volumes of water even if it is not stenothermal.

The needs of spring fishes for quantities of spring flow has also been reported from Alabama (Howell and Black, 1976), Arkansas (Robison and Buchanan, 1988), New Mexico (Hubbs and Echelle, 1972), Oklahoma (Matthews et al., 1985), China, France, Italy, Croatia (Maurice Kottetot, European Ichthyological Congress, pers. comm.), Australia, Brazil, Congo, and Iran. I consider spring fish to be defined as species found wholly or most often in spring heads and/or in the immediate zone downstream (i.e., spring runs) and seldom found elsewhere in the drainage. Many other aquatic organisms have similar spring vs. stream abundances including amphipods (Bowles and Arsuffi, 1993), aquatic plants (Emery, 1967) salamanders (Tupa and Davis, 1976; Chippendale et al., 1993) and crayfish (Hubbs, 2001). I suspect the entire aquatic biota is also involved but commonly not as well known.

EXAMPLES IN *GAMBUSIA*

Gambusia nobilis.—The Pecos gambusia is a relatively robust *Gambusia*, with an arched back and a caudal peduncle depth that is approximately two-thirds of the head length. The margins of the scale pockets are outlined in black and spots are normally absent on the caudal fin, however, sometimes a faint medial row of spots may be present. The dorsal fin has a subbasal row of spots. Females have a prominent black area on the abdomen that surrounds the anus and anal fin. The male gonopodium has a number of unique features including elongated spines on ray 3, small rounded hooks on the tips of rays 4p and 5a, and an elbow on ray 4a consisting of 3 or 4 fused segments located opposite the serrae of ray 4p. *Gambusia nobilis* generally have 8 dorsal, 12 pectoral, 9 to 10 anal, and 6 pelvic rays (Hubbs and Springer, 1957; Koster, 1957; Bednarz, 1975; Echelle and Echelle, 1986). Populations in Toyah Creek (Texas) and Blue Spring (New Mexico) were found to be the most diverse morphologically and genetically and the Toyah Creek population had the greatest genetic heterogeneity (Echelle and Echelle, 1986; Echelle et al., 1989). *Gambusia nobilis* was described by Baird and Girard (1853) based on material from Leon and Comanche springs, Pecos County, Texas. Leon Springs was later designated the type locality (Hubbs and Springer, 1957). The species is endemic to the Pecos River basin in southeastern New Mexico and western Texas and originally ranged from near Fort Sumner, New Mexico to the area around Fort Stockton, Texas. At present, the species is restricted to four main areas, two in New Mexico and two in Texas. Populations live in various springs and sinkholes in Bitter Lake National Wildlife Refuge, near Roswell, New Mexico; Blue Spring, east of Carlsbad Caverns National Park, New Mexico; the Diamond Y springs and draw (= Leon Creek), near Fort Stockton, Texas; and the Balmorhea springs complex and Toyah Creek near Balmorhea, Texas. Extirpated populations include the Pecos River near Fort Sumner and North Spring River in New Mexico, and Leon and Comanche springs, in Texas. Those populations in Comanche Springs were extirpated when the spring dried (Hubbs and Springer, 1957). The population in Leon Springs was eliminated by impoundment (Miller et al., 1991). Those populations in the Balmorhea springs complex and the Diamond Y region are most abundant in stenothermal waters.

Where suitable habitats exist, Pecos gambusia populations can be dense. An estimated 27,000 individuals inhabit the Bitter Lake National Wildlife Refuge area, and 900,000 inhabit Blue Spring (Bednarz, 1975, 1979). Approximately 100,000 Pecos gambusia are estimated to inhabit the Balmorhea springs complex and more than 100,000 in the Diamond Y springs and draw. Pecos gambusia primarily inhabit stenothermal springs, runs, spring-influenced marshes (ciénegas), and irrigation canals carrying spring waters. Some populations however, are also known from areas with little spring influence; these habitats generally have abundant overhead cover, and include sedge covered marshes and gypsum sinkholes (Echelle and Echelle, 1980). One or two other *Gambusia* may also be found in association with *G. nobilis*. Where the western mosquitofish (*G. affinis*) is found, *G. nobilis* inhabits stenothermal waters and *G. affinis* is most often found in eurythermal habitats. Where together, the Pecos gambusia is much more likely to be found associated with vegetation or in deeper waters, while *G. geiseri* tends to be at the surface or in open water over non-vegetated substrates (Hubbs et al., 1995). Another spring endemic, *G. geiseri* was introduced into Pecos gambusia habitat for "mosquito control." This was a serious error as the native *G. nobilis* is at least as good at mosquito control. Pecos gambusia feed relatively non-selectively, consuming a diversity of food types, including amphipods, dipterans, cladocerans, filamentous algae, arachnids and mollusks (Hubbs et al., 1978; Winemiller and Anderson, 1997). *Gambusia nobilis* produce live young. Bednarz (1979) reported that the number of embryos was related to female size and that the mean number of embryos was 38 in the Blue Spring population. Hubbs (1996) found that the birth weight of Pecos gambusia from Texas populations ranged between 35 and 50 mg and females had an interbrood interval of 52 days. Hybrids between *G. nobilis* and *G. affinis* or *G. geiseri* are occasionally found, especially in habitats where one of the species is rare (Hubbs and Springer, 1957).

Pecos gambusia face severe threats from spring flow declines and habitat modification throughout their range. In parts of their range, ciénegas, presumed to have supported large numbers of *G. nobilis*, were drained and spring flows diverted for irrigation. San

Solomon Springs has been modified into a spring-fed swimming pool. During 1998 and 1999, Phantom Lake (part of the Balmorhea springs complex) dried twice and after the second drying, Phantom Lake Spring ceased to flow and ultimately the Phantom Lake Spring refuge canal dried. During May 2000, a pump was installed by the U.S. Bureau of Reclamation to insure continuous flow in the upper spring pool. Additional stresses on the population may occur through competition with the introduced *G. geiseri*. Efforts have been made to improve habitat in the Balmorhea area. A small refugium canal was constructed in 1974 in Balmorhea State Park (Echelle and Hubbs, 1978). In 1993, the Bureau of Reclamation constructed a modified 110-m canal at Phantom Lake Spring (Young et al., 1994) with sloped, sinuous sides to resemble a portion of a ciénega. That canal is now dry and all fish dead as Phantom Lake Spring no longer flows. After Phantom Lake Spring ceased flow and the only water remaining was in the "spring pool" that is artificially maintained by a pump, *G. nobilis* declined precipitously, *G. affinis* increased, and *G. geiseri* remained rather stable (Hubbs, 2001). In cooperation with local residents and farmers, in 1996 the construction of the 1-ha San Solomon Ciénega was completed (McCorkle et al., 1998; Garrett, this volume). This wetland is situated within the boundaries of the original, natural ciénega on state park land. Designed to resemble and function like the original ciénega, the native fish fauna, including *G. nobilis*, has flourished near the inlet where stenothermal conditions prevail. The park refugium canal, and the San Solomon Ciénega have increased numbers and security for the species, but each remains dependent on spring flows.

The Diamond Y introductions of *G. geiseri* were eliminated by efforts to remove exotic *Cyprinodon variegatus* that formed massive hybrid swarms with the endemic *C. bovinus* that threatened the survival of the latter (Hubbs et al., 1978). A byproduct of those control efforts was the eradication of exotic *G. geiseri* from the Diamond Y system. Equivalent collecting effort at Diamond Y Spring before eradication had equal numbers of *G. geiseri* and *G. nobilis*. After eradication, *G. nobilis* had abundances similar to the sum of the two species abundances. Where *G. geiseri* was absent *G. nobilis* dominated stenothermal water and *G. affinis* dominated eurythermal waters. In the Balmorhea area three species are involved. In general the 2 spring species dominate the stenothermal water and *G. affinis* dominates in the eurythermal waters. There is a strong tendency for *G. nobilis* to be restricted to the most stenothermal waters, and *G. geiseri* to be common in waters of intermediate thermal variation. Additional protection for *G. nobilis* stems from its presence in Balmorhea State Park, Bitter Lake National Wildlife Refuge, Diamond Y Draw which is owned by The Nature Conservancy of Texas, and an introduced stock of Pecos gambusia in artificial pools at the Living Desert State Park near Carlsbad, New Mexico.

Gambusia gaigei.— The color pattern of the Big Bend gambusia is weaker than that of the other members of the *G. nobilis* species group. The ground color is silvery with an iridescent blue overtone. There is considerable yellowish-orange on the clear areas of the unpaired fins. The markings on the margins of the scale pockets are faint. There are none anterior to the anus or below the eye. The middorsal streak and dark coloration of the neurocranium cover and obscure the scale-pocket markings, but the postanal streak does not obscure these markings. The faint, broad lateral band often obscures the scale-pocket markings on one scale row. There are a few dark crescents on the scale rows surrounding the lateral band. The anal spot in females is restricted to the anus. The dorsal has a subbasal row of black spots and a dark margin. The caudal has no dark markings. The anal of females has a dark margin; that of males is grayish. There is only a trace of a dark chin bar. Except for the suborbital bar there is no darkening of the lower parts posterior to the eye.

The Big Bend gambusia was described in Hubbs (1929) based on specimens collected by F. M. Gaige from "a marshy cattail slough fed by springs, located close to the Rio Grande at Boquillas, Brewster County, opposite the Mexican village of the same name." Apparently this was the largest river-side spring in the Big Bend region (Hubbs, 1940). Subsequently in June 1954 numerous specimens were obtained from Graham Ranch Warm Springs (Hubbs and Springer, 1957). Graham Ranch Warm Springs (now known as Spring 4) is the largest spring near Boquillas but is 1 km west of Boquillas. Other springs existed at Boquillas that may have been the source of Fred Gaige's captures. Those springs dried in 1954 and no longer contain fish. It is more likely, however, that the original collections came from Graham Ranch Warm Springs.

Although Big Bend gambusia were abundant in Graham Ranch Warm Springs and the newly constructed adjacent "kiddie fishing pool", they were scarce by 1956 and the previously scarce *G. affinis* very abundant. Consequently, renovation efforts were initiated 9 October 1956. Intensive seining obtained 24 individuals and the area was treated with rotenone and fewer than 12 other Big Bend gambusia (and thousands of *G. affinis*) killed (Hubbs and Broderick, 1963). The 24 remaining individuals were placed in 5 locations: 1) Boquillas Spring, Glenn Springs and, stock tank along the Glenn Springs Road (14 individuals); 2) metal tank near the Park Headquarters (6 individuals) and; 3) 4 individuals taken to Austin. The fish placed at location 1 were never seen again. The fish at location 2 flourished until a cold day that killed them all. One of the 4 remaining fish died in Austin but the other 3 (1 female and 2 males) were returned to the park in a newly constructed pond where they flourished (Hubbs and Broderick, 1963). At the same time the Rio Grande Village Camp Ground was established near the Graham Ranch Warm Spring (and the existing 4 springs renamed 1-4). Trees were planted to shade the camp ground and watered from the Rio Grande. That water drained into the Big Bend gambusia pond. *Gambusia affinis* got into those irrigation ditches and subsequently into the Big Bend gambusia pond.

When the pond was examined 16 April 1960 only 27 individuals were obtained. All were taken to Austin. Half of them were sent to the University of Michigan for insurance against extinction. Both cultures flourished, and after a second refuge pond (using Spring 1 water) was constructed, were returned (9 August 1966) to the park (Hubbs and Williams, 1976). With 2 intervals of extreme scarcity, it is not surprising that the surviving population is homozygous (Echelle and Echelle, 1991). Minor problems (introduction of green sunfish, *Lepomis cyanellus*, and minor mortality due to an extremely cold day) did not threaten survival (Hubbs and Williams, 1976). Subsequently all Spring 4 water was diverted to the Campground and the kiddie fishing pool dried. Later a flash flood ran through the Spring 1 refuge pool into the Spring 4 pool, reintroducing the Big Bend gambusia into its original habitat. Increased pumpage caused the Spring 1 refuge pool to overflow through its drain pipe. Fish were transferred from the refuge pool into the overflow ditch and both flourish. Eventually, water leaked from the Spring 4 pool and some Big Bend gambusia occurred in a large beaver pond between Spring 4 and the Rio Grande. Big Bend gambusia flourishes in the 2 spring pools and the Spring 1 drainage ditch. A small population occurs in the Beaver Pond. A small number of *G. affinis* occurs in the Spring 4 pool. The relative number of *G. gaigei* and *G. affinis* is correlated with the thermal stability of the two localities. *G. gaigei* dominates in stenothermal water and *G. affinis* dominates in the eurythermal water (Hubbs, 2001).

In Chihuahua, Mexico a similar pattern emerges but much less data on environmental conditions are available.

Gambusia hurtadoi.—The Dolores gambusia lives in El Ojo de la Hacienda Dolores that has a large spring pool ca 20 X 50 m with a dense population of *G. hurtadoi* as well as an endemic *Cyprinodon*. Both endemics also flourish in the irrigation ditches leaving the spring pool. During wet weather, spring waters empty into the Rio Florido where *G. senilis* is the only gambusia present.

The color pattern of the Dolores gambusia is darker and has more iridescent blue than that of other members of the *G. nobilis* species group. The ground color is iridescent bluish-silver. There is less orange on the body than in *G. alvarezi*. The clear areas on the median fins are yellowish orange. The markings on the margins of the scales are dark but diffuse, and are often obscured by other more prominent markings. There are no marks anterior to the anus and none below the preopercle. The lateral diffusion of the dark middorsal streak often reaches the lateral band. The thin postanal streak does not obscure the scale-pocket markings. The lateral band is broad and dark. The dark crescents on the side are concentrated along the lateral band and often cover and obscure it. They follow the scale-pocket margins. The anal spot is not restricted to the anus. The dorsal fin has a subbasal row of spots, which are darker than the darkened margin. The caudal has no dark markings. The anal fin of females has a dark margin; that of males is grayish. The prominent dark chin bar is often interrupted medially. The suborbital bar is dark.

Three color variants have been noted. These may be designated Spotted, Gray, and Golden. All three lack the dorsal streak, the post-anal streak, and the lateral band. Spotted also has no dark markings on the scale-pockets and no suborbital bar; the color pattern on the body consists chiefly of the crescents which are often grouped and not concentrated along the location of the lateral band. Gray lacks the crescents typical of Spotted. Its coloration somewhat resembles that of *G. geiseri* except that the scale-pocket markings are more diffuse. Golden has no dark markings except the dark margin of the dorsal, three small patches of scale-pocket margins in front of the dorsal and above the pectoral bases, the spotting of the peritoneum, and the dark eye. In life it is an attractive golden yellow. There is no iridescent blue. All three color phases were present in a collection made by Clark Hubbs and Oscar f. Wiegand at El Ojo de la Hacienda Dolores on December 31, 1954. The preserved collection contained a random sample of 1,342 individuals. Later a single Golden individual 16 mm long was collected. Approximately 500 more specimens were collected in the subsequent work. Sixteen Spotted and thirteen Grays have been noted in the preserved sample. Although 502 of the specimens are longer than 20 mm, none of the color variants are. It is possible that they have a reduced survival rate. This hypothesis is supported by our failure to bring the Golden individual back to Austin alive.

Gambusia alvarezi.—The color of the San Gregorio gambusia is more yellow and orange than that of any other members of the *G. nobilis* species group. The ground color is yellow-orange. There is little iridescent blue on the body. All clear areas on the fins are yellow-orange. The diffuse dark markings on the margins of the scales are often obscured by more prominent markings. There are no marks anterior to the anus or below the eye. The middorsal streak is dark, but its lateral diffusion does not reach to the lateral band. The dim postanal streak often obscures the scale-pocket markings. The lateral band is broad and dark. The dark crescentic marks on the side are concentrated along the lateral band. They are not numerous and more than three are seldom interconnected. The lateral band can easily be traced through the areas between the scattered groups of crescents. The black spot around the anus is large. The dorsal fin has a subbasal row of spots and a darker margin. The caudal has no dark markings. The anal fin of females has a dark margin; that of males is uniformly grayish. The prominent dark chin bar is often interrupted medially. The suborbital bar is dark.

Similarly, El Ojo de San Gregorio has a dense population of *G. alvarezi*. El Ojo de San Gregorio has much less volume than El Ojo de la Hacienda Dolores and virtually no spring pool. The water eventually flows (or flowed) into the Rio Parral once occupied by *G. senilis*. Unfortunately the Rio Parral is severely polluted with mining wastes that preclude contact between the two species.

Color differences were maintained in laboratory-reared stocks of *G. alvarezi*, *G. gaigei*, and *G. hurtadoi*.

Gambusia amistadensis.—The Amistad gambusia was a member of the *Gambusia senilis* species group and is closely related to *G. hurtadoi*, *G. alvarezi*, *G. gaigei*, and *G. senilis* (Rauchenberger, 1989). The species is characterized by its relatively slender body, terminal mouth with numerous teeth on each jaw, and males having long serrae on ray 4p of the gonopodium. Preserved specimens have strong crosshatching and numerous darkly pigmented crescent-shaped spots on their scale margins. The mid-dorsal stripe is narrow and the lateral stripe is broad. A short, dusky subocular bar is present. Adult females have a permanent median dark anal spot (Peden, 1973).

The Amistad gambusia was originally described from Goodenough Springs (29°32'10"N, 10°15'10"W) in Val Verde County, Texas. The original range of the species included the headsprings and the 1.3-km spring run downstream to its confluence with the Rio Grande (Peden, 1973). The species became extinct in the wild when Goodenough Springs, once the third largest spring system in Texas, was inundated by Amistad Reservoir when the dam gates were closed in 1968 (Peden, 1973; Brune, 1981). Goodenough Springs and its warm spring run rapidly flowed over limestone gravel and sand substrates along its course to the Rio Grande. Waters originated in the relatively large Edwards-Trinity aquifer (Peckham, 1963) and maintained flow rates of approximately 2,000-4,000 cubic liters per second (Brune, 1981). The type locality and habitat for the Amistad gambusia is now under approximately 30 m of water and former spring openings may now be recharge zones (Peden, 1973; Brune, 1981).

Little is known concerning the food habits of the Amistad gambusia; however, the gut contents of 10 paratypes examined by Peden (1973) contained mostly unidentified items, some insect fragments and traces of filamentous algae. Other fishes co-occurring with the Amistad gambusia prior to the inundation of its habitat included: *Astyanax mexicanus* (Mexican tetra), *Macrhybopsis aestivalis* (speckled dace), *Cyprinella lutrensis* (red shiner), *C. venusta* (blacktail shiner), *C. proserpina* (proserpine shiner), *N. braytoni* (Tamaulipas shiner), *N. jemezanus* (Rio Grande shiner), *Cycleptus elongatus* (blue sucker), *Ictalurus punctatus* (channel catfish), *Ameiurus melas* (black bullhead), *Pylodictis olivaris* (flathead catfish), *Gambusia affinis* (western mosquitofish), *Micropterus salmoides* (largemouth bass), *Lepomis cyanellus* (green sunfish) and *Cichlasoma cyanoguttatum* (Rio Grande cichlid) (Peden, 1973).

Observations in aquaria by Peden (1970, 1973) indicated that male courtship appeared similar to that found in other poeciliids and that pregnant female *Gambusia amistadensis* gave birth to their young in vegetated areas. Of 10 female paratypes examined by Peden (1973), the mean size was 29.8 mm SL (range = 25.9-34.6 mm SL) and 7 contained 5 to 11 (mean 8.9) embryos in each ovary while the other 3 females contained 1 to 7 eggs.

Culture populations of *G. amistadensis* were maintained until the late 1970s at the University of Texas at Austin and at the U.S. Fish and Wildlife Service's endangered species culture facility in Dexter, New Mexico (Hubbs and Jensen, 1984). These populations were contaminated by western mosquitofish (*Gambusia affinis*), which eliminated the *G. amistadensis* in these cultures prior to 1983 (Hubbs and Jensen, 1984). I suspect this species would not be extinct if those refugia had been maintained as stenothermal environments.

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Address of author:

CLARK HUBBS

Integrative Biology
The University of Texas at Austin
Austin, TX 78712