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DISTRIBUTION AND STATUS OF THE DEVILS RIVER MINNOW, *DIONDA DIABOLI*

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ABSTRACT—Recent collections made throughout the historic range of *Dionda diaboli* (Devils River minnow) in the United States showed a decline in the range and relative abundance of this species. In the few remaining places where *D. diaboli* was found, its population size typically comprised <1% of the fish community. Also, a general reduction in relative abundance of species associated with flowing-water environments was evident while those species associated with more lentic habitats appeared to be increasing in number.

Members of the genus *Dionda* are typically found in lotic habitats in southwestern North America. Their distributional patterns in these habitats are somewhat unusual in that there are several instances of sympatric associations of species pairs, with each species pair distributed allopatrically to the others (Mayden et al., in press).

Dionda diaboli (Devils River minnow; Hubbs and Brown, 1956) occurs sympatrically with *D. argentosa* (manantial roundnose minnow, a name we herein propose as the official American Fisheries Society common name) throughout most of its range. These fishes are found primarily in channels of fast-flowing, spring-fed water over gravel bottoms (Harrell, 1978). *Dionda argentosa*, previously assigned to the *D. episcopa* (roundnose minnow) complex, has since been elevated to species status (Mayden et al., in press). These two species can be distinguished morphologically (Hubbs and Brown, 1956) and electrophoretically (Mayden et al., in press).

Dionda diaboli is known historically from the Devils River, San Felipe, and Sycamore creeks, Val Verde Co., Texas, and Las Moras Creek, Kinney Co., Texas. It evidently has been extirpated from Las Moras Creek (Smith and Miller, 1986). *Dionda argentosa* occurs in the first three localities but has never been reported from Las Moras Creek. There are records of *D. diaboli* from two small streams in Mexico, the Rio San Carlos and Rio Sabinas, but they seem to be rare in these locations (Miller, 1978; S. Contreras-Balderas, pers. comm.).

The regional climate is semi-arid, without sufficient precipitation for non-irrigation farming. Precipitation is usually in the form of brief showers and thunderstorms, often of such intensity as to result in flash flooding, with 80% falling between April and October (National Oceanographic and Atmospheric Administration, 1989). During our study, data from United States Weather Bureau stations in Del Rio and Brackettville revealed that the region was experiencing a drought, although not as severe as the one that occurred in Texas between 1947 and 1957. Del Rio recorded below-average precipitation for 9 of 15 years from 1975 through 1989, with an average annual deficit from the average rainfall since 1906 of 10.13 (± 6.22) cm. Comparable data from Brackettville showed an average annual deficit for the last 10 years of 10.04 (± 5.94) cm from the previous 30-year average. Efforts to ameliorate the effects of drought on water available for human consumption (e.g., stream channelization, impoundment, and groundwater pumping) have combined to alter stream-flow patterns (Hubbs, 1990); many of the perennial streams of the region (Gray, 1919) no longer flow.

Because of its restricted range and low numbers, *D. diaboli* is listed as threatened by the Texas Parks and Wildlife Department. This species is also listed as threatened by the Texas Organization for Endangered Species and as a Category 2 species (considered for listing as endangered or threatened) by the United States Fish and Wildlife Service (United States Department of the In-

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TABLE 1.—List of collection localities. The 1953 collections were by W. H. Brown, Texas Game and Fish Commission. The rest are comprised of various field collections by the authors and their colleagues. Site numbers refer to those listed in Table 2.

Site no.	Date	Location	Map coordinates
1	1953, 1989	Devils River at Baker's Crossing	29°57'50"N, 101°08'41"W
2	1989	Devils River at Blue Spring	29°53'38"N, 100°59'39"W
3	1979, 1980, 1989	Dolan Creek at Dolan Springs	29°53'48"N, 100°59'03"W
4	1989	Mid-Dolan Creek	29°53'25"N, 100°59'02"W
5	1989	Dolan Creek near Devils River confluence	29°53'09"N, 100°59'33"W
6	1953, 1979	Devils River at Pafford's Crossing	29°40'40"N, 101°00'05"W
7	1989	Rio Grande upstream of Del Rio	29°22'43"N, 101°00'47"W
8	1989	Upper Cienegas Creek	29°21'25"N, 100°56'25"W
9	1989	Lower Cienegas Creek	29°20'58"N, 100°56'40"W
10	1979, 1989	Outflow from Head Springs of San Felipe Creek, Hinds Ranch	29°23'54"N, 100°52'05"W
11	1979	Downstream of Head Springs of San Felipe Creek, Lowe Ranch	29°22'47"N, 100°52'53"W
12	1979	San Felipe Creek, upstream of U.S. Highway 277	29°22'05"N, 100°53'00"W
13	1989	San Felipe Creek at U.S. Highway 277	29°22'00"N, 100°53'05"W
14	1989	San Felipe Creek at Canal Street in Del Rio	29°21'20"N, 100°53'45"W
15	1989	San Felipe Creek, 4.5 km upstream of mouth (below sewage treatment plants)	29°19'52"N, 100°53'20"W
16	1989	Sacatosa Creek at impounded headspring	29°22'00"N, 100°45'26"W
17	1988, 1989	Sycamore Creek at U.S. Highway 277	29°15'14"N, 100°45'02"W
18	1989	Mud Springs (impoundment and downstream)	29°27'34"N, 100°37'17"W
19	1989	Mud Creek, 4.5 km upstream of U.S. Highway 90	29°23'54"N, 100°39'20"W
20	1989	Mud Creek at U.S. Highway 90	29°22'45"N, 100°40'17"W
21	1989	Mud Creek upstream of Sycamore Creek confluence	29°16'33"N, 100°44'25"W
22	1989	Pinto Creek at FM 2804	29°22'10"N, 100°29'28"W
23	1989	Pinto Creek at U.S. Highway 90	29°20'10"N, 100°31'58"W
24	1989	Pinto Creek at FM 3008	29°17'47"N, 100°36'10"W
25	1988, 1989	Pinto Creek at U.S. Highway 277	29°11'20"N, 100°42'10"W
26	1979, 1989	Las Moras Creek at Las Moras Springs in Brackettville	29°18'25"N, 100°24'55"N
27	1989	Las Moras Creek near FM 1572, Salado Seco Ranch	29°07'20"N, 100°32'16"W
28	1988	Las Moras Creek at U.S. Highway 277	29°00'16"N, 100°38'20"W

terior, 1989). The purpose of this study is to document current distribution and relative abundance of *D. diabolus* throughout its range in the United States.

MATERIALS AND METHODS.—To determine occurrence and relative abundance, collections were made during April, July, and October 1989 throughout the historic range of *D. diabolus* in the United States. Unpublished, early records and previous collections by the authors were used for comparisons (Table 1). Water-

sheds sampled during the present study included all known localities in the United States for *D. diabolus* as well as other adjacent sites.

Collecting methods used in the present study were similar to those used by the authors in previous collections where samples were taken for at least 1 h at each site with 3- to 5-m long, 5- to 6-mm mesh seines. All habitats were thoroughly sampled (typically 100- to 200-m stream stretches). This method was employed to obtain a sample representative of the relative abundance of all fish species at each site.

All fishes collected were preserved in the field and identified and counted in the laboratory. Relative abundances of all species were calculated (Table 2) to determine whether differences in population sizes among the various sites influenced the distribution of *D. diaboli*. Comparisons of actual abundances of species over time were not feasible because effort (e.g., time per unit area) was not quantified. Fishes such as *D. diaboli* are very habitat specific and, therefore, changes in habitat affect their abundance. Rather than limit collections to designated times in predetermined locations, we opted for thorough sampling of available habitats to better characterize fish communities at each station. To detect the effect of changes in diversities among sites, the Shannon index of species diversity (H' ; Shannon and Weaver, 1949) was calculated for each collection (Table 2).

Principal components analysis was performed on the relative abundance of the 21 most abundant species (each having >50 individuals captured from all sites) to determine if the overall pattern of variation in species abundances could be reduced to a smaller subset of interpretable components (Table 3). Percent relative abundances of each of the 21 most abundant species was transformed using a standard arcsine transformation, and the extracted principal components were rotated orthogonally by the varimax procedure, which maximizes the proportion of the original data variance associated with the resulting eigenvectors.

RESULTS AND DISCUSSION—*Dionda diaboli* were seldom encountered during this study. The apparent reduction in range and abundance seemed to be associated with changes in other species and their habitat.

Devils River—In Brown's 1953 collection at Baker's Crossing, *D. diaboli* was the fifth most abundant species (site 1, Table 2). During the mid-1970s, it was reported to be the sixth most abundant fish species in the Devils River (Harrell, 1978). Collections from this study indicated *D. diaboli* was rare and one of the least abundant fish species in the Devils River. As recently as 1988, Mayden et al. (in press) collected 20 specimens of *D. diaboli* at Baker's Crossing on the Devils River. One *D. diaboli* was collected near Baker's Crossing during this study. It was obtained downstream of the crossing in an area of emergent vegetation and apparent spring seeps.

Approximately 100 *D. diaboli* were collected in November 1988 at Finegan Springs on the Devils River (Hubbs and Garrett, 1990). This location is about 1.5 km north of the Dolan Creek confluence with the Devils River. Individual *D. diaboli* were collected only in the area where the

spring runs entered the river, whereas individual *D. argentosa* were collected in adjacent locations. Results of subsequent collections have varied greatly. In October 1989, only one *D. diaboli* was taken in this location, while a collection in August 1990 yielded approximately 50 individuals (not retained; C. Hubbs, pers. comm.), and a collection by G. P. Garrett in October 1990 yielded no *D. diaboli*.

Blue Spring and its spring run into the Devils River yielded no *D. diaboli* and few *D. argentosa* during this study (site 2, Table 2). The remainder of the species composition was, however, similar to that of the Finegan Springs area.

Dolan Creek—Although *D. argentosa* is common throughout Dolan Creek and at times abundant (sites 3 and 4, Table 2), only one *D. diaboli* has ever been taken from this locality. The creek is easily accessible by fish from the river and the habitat appears appropriate for *D. diaboli*.

Rio Grande—*Dionda diaboli* has access to the Rio Grande, yet none had been captured or reported from there. The Rio Grande may have served historically as an avenue of dispersal and recolonization of watersheds within the range of the species. The alteration of habitat caused by construction of Amistad Reservoir makes it unlikely that there would now be movement in or out of the Devils River. Although all habitats were sampled extensively, the portion of the Rio Grande immediately downstream of Amistad Dam (site 7, Table 2) appeared depauperate of fishes.

Cienegas Creek—Neither *D. argentosa* nor *D. diaboli* have been reported from Cienegas Creek, and none was captured during this study (sites 8 and 9, Table 2). The small size and general conditions of this creek, as well as the species composition of captured fishes, are more similar to small Balconian province streams downstream from the main spring runs than to the upper, heavily spring-influenced runs where *Dionda* typically abound.

San Felipe Creek—In the 1979 collections, *D. diaboli* comprised 6 to 18% of the *Dionda* present in the headwaters of San Felipe Creek (sites 10 and 11, Table 2). Collecting in the Head Spring area during this study (site 10, Table 2) yielded no *D. diaboli*. Relative abundances of other species collected, except *Gambusia affinis* (western mosquitofish) were similar to those in previous collections. Reduced flow rates from these springs may have contributed to a reduction in abundance of *G. affinis* and *D. diaboli*. The downstream

TABLE 2.—Relative abundances (percent) of fishes captured during trans-Pecos area collections. Site localities are listed in Table 1. Introduced species are indicated with an asterisk.

Species	Collection site											
	1		2		3		4		5		6	
	1953	1989	1989	1979	1980	1989	1989	1989	1953	1979	1989	1989
<i>Lepisosteus oculatus</i>												
<i>L. osseus</i>										<1		
<i>Dorosoma cepedianum</i>												
<i>D. petenense</i>												
<i>Astyanax mexicanus</i>	<1	2		6	16	3	16		<1	1		4
<i>Camptostoma anomalum</i>									<1	1		
<i>Cyprinus carpio</i> *												
<i>Cyprinella lutrensis</i>												
<i>C. lutrensis</i> ×												
<i>C. venusta</i> hybrid												
<i>C. proserpina</i>	7	2	9	17	1				11	30		
<i>C. venusta</i>	59	18	19						5	23		50
<i>Dionda argentosa</i>	12	35	1	24	70	60	20		27	7		
<i>D. diaboli</i>	5	<1				1						
<i>Notropis amabilis</i>	6	21	63	2		11			1	4		39
<i>N. braytoni</i>												
<i>N. jemezianus</i>	<1								1			
<i>N. stramineus</i>	2	1								<1		
<i>Pimephales vigilax</i>									<1	2	67	
<i>Carpodacus carpio</i>				<1	<1							
<i>Ictiobus bubalus</i>												
<i>Moxostoma congestum</i>	<1	1		<1					<1	1	28	4
<i>Ictalurus furcatus</i>												
<i>I. lupus</i>					<1							
<i>I. melas</i> *												
<i>I. natalis</i>												
<i>I. punctatus</i>	1								<1	<1		
<i>Pylodictis olivaris</i>	<1											
<i>Cyprinodon eximius</i>					<1	14	23	24	<1	11		
<i>Fundulus grandis</i> *		<1										
<i>Gambusia affinis</i>	3	15	5	40	4	9	39	63	30	12	4	
<i>G. senilis</i>									1			
<i>Poecilia latipinna</i> *												
<i>Menidia beryllina</i> *										2		
<i>Lepomis auritus</i> *	1	1							1	1		2
<i>L. cyanellus</i>	<1		<1							1		
<i>L. gulosus</i>									<1			
<i>L. macrochirus</i>									10			
<i>L. megalotis</i>	1	2	2	<1	3	1	1	12	2	<1		
<i>L. microlophus</i> *												
<i>Micropterus dolomieu</i> *										<1		
<i>M. salmoides</i>	<1	1		1	<1					<1		2
<i>Pomoxis annularis</i>												
<i>Etheostoma grahami</i>	1			8	2				<1	<1	1	
<i>Cichlasoma cyanoguttatum</i>	3	2	2	1	2	1			9	2		
<i>Tilapia aurea</i> *												
Number captured	1,277	378	273	989	4,336	145	69	41	831	3,009	97	56
Species diversity (H')	2.2	2.5	1.7	2.3	1.5	1.8	2.0	1.3	2.8	3.0	1.1	1.6
Introduced species (%)	6	14	0	0	0	0	0	0	5	14	0	17

Species	Collection site											
	9	10		11	12	13	14	15	16	17		18
	1989	1979	1989	1979	1979	1989	1989	1989	1989	1988	1989	1989
<i>Lepisosteus oculatus</i>												
<i>L. osseus</i>												
<i>Dorosoma cepedianum</i>												
<i>D. pelenense</i>											3	
<i>Astyanax mexicanus</i>	3	3	12	1	8	7	3	6		2	<1	11
<i>Campostoma anomalum</i>										<1		
<i>Cyprinus carpio</i> *											<1	
<i>Cyprinella lutrensis</i>										<1	<1	2
<i>C. lutrensis</i> ×												
<i>C. venusta</i> hybrid											<1	
<i>C. proserpina</i>		1	<1	9		1	12					
<i>C. venusta</i>	73	<1	<1	11	9	1	3	34		<1	1	
<i>Dionda argentosa</i>		37	37	7	3	38	6			12	36	
<i>D. diaboli</i>		2		2	1	<1	<1			<1	<1	
<i>Notropis amabilis</i>	2	12	43	41	61	14	59	54		<1	6	22
<i>N. braytoni</i>										2		
<i>N. jemezianus</i>												
<i>N. stramineus</i>												
<i>Pimephales vigilax</i>										<1		
<i>Carpionodes carpio</i>												
<i>Ictiobus bubalus</i>				<1								
<i>Moxostoma congestum</i>	1			<1	<1						3	
<i>Ictalurus furcatus</i>											<1	
<i>I. lupus</i>											<1	
<i>I. melas</i> *										<1		
<i>I. natalis</i>				<1	<1	<1	<1				2	
<i>I. punctatus</i>				<1	1							
<i>Pylodictis olivaris</i>												
<i>Cyprinodon eximius</i>												
<i>Fundulus grandis</i> *												
<i>Gambusia affinis</i>	6	39	3	22	3	17	15		16	80	1	62
<i>G. senilis</i>												
<i>Poecilia latipinna</i> *												
<i>Menidia beryllina</i> *												
<i>Lepomis auritus</i> *	3									<1	1	
<i>L. cyanellus</i>		1		<1							<1	
<i>L. gulosus</i>												
<i>L. macrochirus</i>	<1								49	<1		
<i>L. megalotis</i>		1		1	3	1	<1			<1	3	
<i>L. microlophus</i> *												
<i>Micropterus dolomieu</i> *												
<i>M. salmoides</i>	2		<1	<1	2		<1		25	<1	3	<1
<i>Pomoxis annularis</i>												
<i>Etheostoma grahami</i>		1	5	2	6	16	<1			<1	<1	
<i>Cichlasoma cyanoguttatum</i>	4	3		2	2	4	2	6	10	1	1	2
<i>Tilapia aurea</i> *	7									1	38	<1
Number captured	550	1,214	276	2,244	265	587	1,064	35	104	1,243	1,266	413
Species diversity (H')	1.6	2.1	1.8	2.5	2.2	2.5	1.9	1.5	1.8	1.2	2.4	1.6
Introduced species (%)	20	0	0	0	0	0	0	0	0	17	14	14

TABLE 2—Continued.

Species	Collection site											
	19	20	21	22	23	24	25	26	27	28		
	1989	1989	1989	1989	1989	1989	1988	1989	1979	1989	1989	1988
<i>Lepisosteus oculatus</i>								1				
<i>L. osseus</i>			<1								1	1
<i>Dorosoma cepedianum</i>			6									
<i>D. petenense</i>												
<i>Astyanax mexicanus</i>	50		5	2	5	3	9		21	1	9	15
<i>Camptostoma anomalum</i>												1
<i>Cyprinus carpio</i> *												
<i>Cyprinella lutrensis</i>		6	20	6	62	54	19	2			23	19
<i>C. lutrensis</i> ×												
<i>C. venusta</i> hybrid					1			3			7	6
<i>C. proserpina</i>												
<i>C. venusta</i>					<1		53	16	25	6	30	27
<i>Dionda argentosa</i>								2				
<i>D. diaboli</i>												
<i>Notropis amabilis</i>	8		1	15	<1							12
<i>N. braytoni</i>			1									
<i>N. jemezianus</i>												
<i>N. stramineus</i>								55				
<i>Pimephales vigilax</i>			22									1
<i>Carpionodes carpio</i>												
<i>Ictiobus bubalus</i>												
<i>Moxostoma congestum</i>												
<i>Ictalurus furcatus</i>												
<i>I. lupus</i>					2						14	
<i>I. melas</i> *												
<i>I. natalis</i>												
<i>I. punctatus</i>			1		1	4		3			6	
<i>Pylodictis olivaris</i>												
<i>Cyprinodon eximius</i>												
<i>Fundulus grandis</i> *												
<i>Gambusia affinis</i>		45	13	48	16	12		10	20	76	6	1
<i>G. senilis</i>												
<i>Poecilia latipinna</i> *					1			13	4			
<i>Menidia beryllina</i> *												
<i>Lepomis auritus</i> *					1	<1		3				
<i>L. cyanellus</i>			4	<1								1
<i>L. gulosus</i>												
<i>L. macrochirus</i>	25	6	26	4	<1		3		2		3	7
<i>L. megalotis</i>		6	3		2		13	3	5	2		9
<i>L. microlophus</i> *								<1				
<i>Micropterus dolomieu</i> *												
<i>M. salmoides</i>		4		6	2	6	3	2	3	1		1
<i>Pomoxis annularis</i>											1	
<i>Etheostoma grahami</i>												
<i>Cichlasoma cyanoguttatum</i>	17	10	1	19	8	21		2	5	4		2
<i>Tilapia aurea</i> *		18								7		
Number captured	12	67	295	48	373	206	32	346	91	143	70	168
Species diversity (H')	1.7	2.0	2.7	2.2	2.0	1.9	2.0	2.2	2.8	1.4	2.8	2.9
Introduced species (%)	0	13	0	0	14	14	0	18	10	25	0	7

TABLE 3.—Summary statistics from principal components analysis (varimax rotation) of the 21 most abundant species captured during 36 historic and recent seine collections in the trans-Pecos area of Texas.

Species	Eigenvectors							
	1	2	3	4	5	6	7	8
<i>Astyanax mexicanus</i>	-0.15	-0.23	0.14	-0.02	-0.21	-0.03	-0.69	-0.27
<i>Cyprinella lutrensis</i>	-0.33	-0.03	-0.06	0.06	-0.21	0.72	-0.07	0.07
<i>C. proserpina</i>	0.35	-0.02	0.03	0.06	0.78	-0.09	-0.04	-0.01
<i>C. venusta</i>	-0.03	-0.10	0.85	-0.14	0.14	0.17	0.14	0.17
<i>Dionda argentosa</i>	0.64	-0.11	-0.23	-0.13	0.07	-0.37	-0.10	0.10
<i>D. diaboli</i>	0.75	-0.12	0.09	0.01	-0.02	0.11	0.12	-0.01
<i>Notropis amabilis</i>	0.41	-0.13	0.47	0.22	0.09	-0.35	-0.07	-0.34
<i>N. stramineus</i>	0.02	-0.05	0.05	-0.03	-0.05	-0.03	-0.04	0.91
<i>Pimephales vigilax</i>	-0.12	0.94	-0.11	-0.05	0.00	0.03	-0.08	-0.03
<i>Moxostoma congestum</i>	0.04	0.90	0.16	0.02	0.06	-0.11	0.22	0.01
<i>Ictalurus punctatus</i>	0.11	-0.08	0.14	0.09	0.08	0.87	-0.09	-0.05
<i>Cyprinodon eximius</i>	-0.11	-0.10	-0.31	-0.67	0.38	-0.14	-0.06	-0.03
<i>Gambusia affinis</i>	0.05	-0.18	-0.74	-0.11	0.10	0.02	0.29	-0.10
<i>Menidia beryllina</i>	-0.14	0.07	0.03	-0.09	0.88	0.00	-0.01	0.05
<i>Lepomis auritus</i>	-0.03	0.02	0.34	0.09	0.18	0.05	0.40	0.67
<i>L. macrochirus</i>	-0.61	-0.05	-0.16	0.39	-0.13	-0.02	-0.22	-0.05
<i>L. megalotis</i>	-0.16	-0.23	-0.08	-0.61	-0.26	0.11	0.13	0.08
<i>Micropterus salmoides</i>	-0.38	-0.19	-0.11	0.53	-0.18	0.10	0.30	0.16
<i>Etheostoma grahami</i>	0.71	0.13	-0.14	0.17	0.03	-0.16	-0.25	-0.07
<i>Cichlasoma cyanoguttatum</i>	-0.23	-0.33	-0.20	0.70	0.02	0.20	0.06	0.00
<i>Tilapia aurea</i>	-0.11	-0.03	-0.02	0.02	-0.21	-0.17	0.77	-0.07
Eigenvalue	3.380	2.348	2.146	1.928	1.742	1.532	1.245	1.045
% variance explained	16.1	11.2	10.2	9.2	8.3	7.3	5.9	5.0
Cumulative % variance explained	16.1	27.3	37.5	46.7	55.0	62.3	68.2	73.2

springs on the Lowe Ranch (site 11, Table 2) were not accessed, and, therefore, recent presence of *D. diaboli* there is unknown.

In the United States Highway 277 area of San Felipe Creek (site 13, Table 2), numbers of *D. diaboli* were similar to those in the 1979 collection (site 12, Table 1), but the relative abundance of *D. argentosa* had increased significantly. We collected small *Dionda* in beds of submerged vegetation and larger adults in open-water current nearby. Numbers for other taxa varied but were generally similar between the 1979 and 1989 collections.

The Canal Street location (site 14, Table 2) had both species of *Dionda* in beds of submergent vegetation adjacent to the road crossing. The stream was sampled for approximately 100 m upstream and downstream from this location, but no more *Dionda* were obtained.

The downstream location (site 15, Table 2) was characterized by deep, swift-flowing water,

a narrow stream bed, and steeply-cut, mud banks. Habitat did not appear suitable for *Dionda*, and none was collected.

Sacatosa Creek—No *Dionda* had been reported from Sacatosa Creek. None was captured during this study.

Sycamore Creek—This location was not listed in most *D. diaboli* distribution accounts (e.g., Hubbs and Brown, 1956; Hubbs, 1957; Harrell, 1978; Williams et al., 1985), but it has been collected there (site 17, Table 2). The creek was first listed as part of the range by Harrell (1980).

There was no surface flow in Sycamore Creek during our study. *Dionda diaboli* was collected from one of four disconnected, stagnant pools near the United States Highway 277 crossing. Water was provided by subsurface flow, primarily from Mud Creek, but the pools were obviously drying up.

Mud Creek—Mud Springs has continued to flow during the present drought and, according

to the landowner, remained flowing during the drought in the 1950s. Although the springs are impounded, the area immediately downstream of the outflow appears to support appropriate habitat for *Dionda*, yet neither *D. diaboli* nor *D. argentosa* were taken at any location on Mud Creek (sites 18 to 21, Table 2). This is particularly surprising because of the presence of both species in Sycamore Creek <3 km downstream of the confluence with Mud Creek.

Pinto Creek—*Dionda diaboli* has not been previously reported from Pinto Creek, and none was captured there in this study (sites 22 to 25, Table 2). This creek does, however, support *D. argentosa*. The creek environments sampled consisted of either very shallow water over bedrock or heavily vegetated, slow-moving waters. The general conditions of Pinto Creek were not typical of headwater spring-influenced runs where *D. diaboli* has historically been found.

Las Moras Creek—Although *D. diaboli* formerly occurred in Las Moras Creek, it was not collected there in 1979 (site 26, Table 2) and evidently has been extirpated from this locality (Smith and Miller, 1986). Our recent collections confirm this conclusion (sites 26 and 27, Table 2). Stream flow has been greatly reduced by drought and diversion of water for human consumption. The springs reportedly ceased flowing in the early 1960s and again in 1980 (R. T. Brown, pers. comm.). Additionally, the headsprings area has been heavily impacted through channelization, impoundment, and diversion of water to supply swimming pools at Fort Clark Springs Resort. The water flowing out of the impounded headsprings into the creek smelled strongly of chlorine during our sampling.

Overview—Comparing the relative abundances of the most numerous species taken during the collections on record (including this study) revealed a pattern to some of the temporal changes. There has been a general increase in the relative abundance of species that tend to occupy quiet water or pool environments (e.g., clupeids, poeciliids, and centrarchids), conditions that are often limited in flowing spring runs. Consistent with this trend were significant increases in relative abundance of introduced *Tilapia aurea* (blue tilapia). We hypothesize that the current drought has enhanced conditions for these species by reducing stream flow and causing a proportional increase in pool environments. This situation has been apparently exacerbated by human modifi-

cations to stream habitats and was most evident in the two streams that have suffered the greatest degree of impact, Sycamore and Las Moras creeks.

One apparent contradiction to this pattern is an increase in *Notropis amabilis* (Texas shiner), a species typically found in spring and headwater environments (Gilbert, 1980). The increased relative abundance of this species may be due to its ability to take advantage of some component of the changed environment not available to other lotic fish taxa. Harrell (1978) found this species to be more environmentally versatile in the Devils River, in that it predominated in habitats intermediate between channels and pools.

Diversity index measures (Table 2) were similar through time and among localities, although a general decline over time was noted. There were no obvious correlations found for occurrence or abundance of *D. diaboli*. This species has been found in some of the most speciose environments as well as those with much less diversity.

Because *D. diaboli* was infrequently encountered, the principal components analysis was thought to allow insight into occurrence patterns by revealing species and habitat associations. The principal components analysis identified eight significant factors which accounted for about 73% of the observed variation in species' relative abundances (Table 3). *Dionda diaboli* was positively associated with *Cyprinella proserpina* (proserpine shiner), *D. argentosa*, *N. amabilis*, and *Etheostoma grahami* (Rio Grande darter). These species commonly inhabit the moving water channels of clear spring runs. Hubbs and Brown (1956) found *D. diaboli* in greater abundance than *D. argentosa* only at Baker's Crossing on the Devils River. It seems that, when in sympatry with *D. argentosa*, *D. diaboli* has a competitive advantage only under very specific conditions. Relative abundance of *D. diaboli* had a negative association with the abundance of *Cyprinella lutrensis* (red shiner), *Lepomis macrochirus* (bluegill), and *Micropterus salmoides* (largemouth bass), species most commonly encountered in slower-moving water or deeper pools. These findings are in general agreement with the pattern described by Harrell (1978) concerning the swift-water, main-channel distribution patterns of *D. diaboli* and associated species in the Devils River.

In conclusion, *D. diaboli* faces a number of threats to its survival. This species has historically occupied a restricted natural range at the southwestern edge of the Balconian province. The range

has been reduced through the inundation of the lower portion of the Devils River by Amistad Reservoir and the extirpation of the Las Moras Creek population. The latter was probably due to habitat changes associated with recreational use of the headsprings and dewatering of the creek. Elsewhere within their range, *D. diaboli* also appears to have declined in abundance. Although the exact reasons are not known at each locality, reduction in water flow from human use and drought probably is a major contributing factor.

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