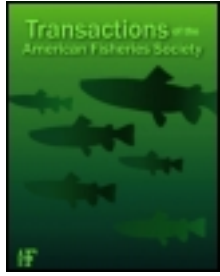


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### Site Fidelity and Movement of *Etheostoma fonticola* with Implications to Endangered Species Management

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ARTICLE

## Site Fidelity and Movement of *Etheostoma fonticola* with Implications to Endangered Species Management

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### Abstract

We quantified site fidelity, directionality and magnitude of movement, and factors associated with movement of the endangered Fountain Darter *Etheostoma fonticola*, a narrowly distributed (<11 km of stream habitat) and small etheostomid, within a 200-m section of a spring-fed river on the Edwards Plateau of south-central Texas. *Etheostoma fonticola* exhibited high site fidelity, moving on average ( $\pm 1$  SD)  $10 \pm 17$  m during a 1-year period. Site fidelity was most notable in areas with low-growing aquatic vegetation (i.e., algae or *Riccia fluitans*). Movement was most often towards areas with low-growing aquatic vegetation (69%), more frequently in an upstream direction (81%), in winter and spring–summer seasons (>55%), and among larger fish (>30 mm TL). Maximum distance moved was 95 m within 26 d. Movement of *E. fonticola* was consistent with movement of narrowly distributed and slackwater etheostomids as well as widely distributed, swift-water etheostomids. As such, movement potential and maximum movement do not satisfactorily explain why some darters are more widely distributed than others. Collectively, etheostomids conform to the theory of restricted movements among resident stream fishes, but movement of large distances occurs and is probably necessary, even among species with high site fidelity.

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Instream movement of small-bodied, freshwater fishes enables species persistence in lotic systems under a variety of environmental conditions (Meffe 1984), maintenance of genetic connectivity and life history requirements (Hall et al. 1991; Johnston 2000; Hutchings and Gerber 2002), and recolonization of areas after episodes of spates or dewatering (Labbe

and Fausch 2000). However, under a range of average hydrological conditions, small-bodied fishes are relatively sedentary and move <50 m (Gerking 1953). The restricted-movement paradigm (Gerking 1959; Gowan et al. 1994) describes the general pattern of limited instream movement and is supported for several species, including cyprinids (Johnston 2000; Belica and

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Rahel 2008), cottids (Brown and Downhower 1982; Knaepkens et al. 2004; Petty and Grossman 2004; Hudy and Shiflet 2009), centrarchids (Gerking 1953), and percids (Freeman 1995; Roberts and Angermeier 2007). Recent studies expand the restricted-movement paradigm to include heterogeneity in movement by small proportions of conspecifics within high site fidelity populations, and although it is not known whether these individuals are genetically predisposed to movement or stimulated by environmental triggers, they are probably essential to population persistence (Smithson and Johnston 1999; Skalski and Gilliam 2000; Roberts et al. 2008; Breen et al. 2009).

Restricted movement, small body sizes, and long-term environmental stability are interrelated with high rates of species diversification in North America, especially among the family Percidae (Smith 1981). In central and eastern North America, darter (genera *Percina*, *Ammocrypta*, and *Etheostoma*) richness is highest in unglaciated drainages of the Mississippi River drainage ( $N = 87$ ), Gulf Slope drainages ( $N = 48$ ), and Atlantic drainages ( $N = 28$ ) (Page 1983). With small body sizes and restricted movements, percentages of darters endemic to a drainage range from 44% in the Gulf Slope drainages to 64% in the Atlantic drainages. Restricted movements and narrow distributional ranges make these taxa susceptible to anthropogenic alterations. Currently, 44% of percids are considered imperiled (Jelks et al. 2008). Therefore, greater understanding of the quantification of darter movement is needed not only to assess anthropogenic effects on populations (i.e., habitat degradation, instream flow alterations, instream barriers, and fragmentation) for conservation measures but also to support the premise that small body fishes, such as the darters, conform to the restricted-movement paradigm.

*Etheostoma*, the smallest in TL and the most derived genera of darters, inhabit small to large sloughs, creeks, and rivers in slackwater to swift-flowing mesohabitats (Ultsch et al. 1978). Site fidelity among etheostomids is high, with 80–97% of individuals remaining within the habitat patch of initial capture during a period of up to 1 year (Mundahl and Ingersoll 1983; Boschung and Nieland 1986; Labbe and Fausch 2000; Roberts and Angermeier 2007). Mean distance moved is <200 m (Mundahl and Ingersoll 1983; Roberts and Angermeier 2007), and maximum distance traveled is up to 3 km (Boschung and Nieland 1986). Direction of movement is biased towards upstream (Mundahl and Ingersoll 1983; Labbe and Fausch 2000; Roberts and Angermeier 2007) at times by older fish (Labbe and Fausch 2000) and other times by younger fish (Roberts and Angermeier 2007). Factors associated with movement are speculative, but instream movement generally occurs more often during nonreproductive periods (Scalet 1973; Mundahl and Ingersoll 1983), ontogenetic shifts in habitat associations (Labbe and Fausch 2000), and times of declining habitat quality (Mundahl and Ingersoll 1983; Roberts and Angermeier 2007). Among published studies, no discernible pattern in site fidelity or movement has been noted between narrowly distributed *Etheostoma* (*E. boschungi*, *E. cragini*, *E. podostemone*) and widely distributed *Etheostoma* (i.e., *E. flabellare*,

*E. nigrum*) or between swift-water and riffle-associated species (*E. flabellare*, *E. podostemone*) and slackwater-associated species (*E. boschungi*, *E. cragini*, *E. nigrum*).

The Fountain Darter *E. fonticola*, a U.S. federally listed endangered species, is endemic to the Guadalupe River basin of central Texas and is currently restricted to two populations in a total of 11 km of stream habitat (Schenck and Whiteside 1976). Considered the smallest species of *Etheostoma* (Page 1983), *E. fonticola* persist in high-volume spring outflows and headwater reaches of the Comal River (1928–2011 daily discharge: mean, 8.8 m<sup>3</sup>/s; range, 0.2–620 m<sup>3</sup>/s; U.S. Geological Survey [USGS] station 08169000) and the San Marcos River (1994–2011 daily discharge: mean, 5.6 m<sup>3</sup>/s; range, 2.4–175 m<sup>3</sup>/s; USGS station 08170500). Instream habitat is fragmented by low-head dams or culverts. As it is the smallest darter and is a representative of the narrowly distributed *Etheostoma* genus, we predicted that *E. fonticola* would be highly sedentary with limited instream movement. Furthermore, we predicted that the *E. fonticola* would be sedentary year round, because it is one of the few North American fishes to spawn year round (Schenck and Whiteside 1977). When movement does occur, it is biased towards upstream. Specific objectives of this study were to assess level of site fidelity, quantify directionality and magnitude of movement, and correlate biotic and abiotic factors associated with movement of *E. fonticola* within a section of the Comal River. Implications of this study will inform various aspects of endangered species and habitat management within the Comal and San Marcos rivers, including assessing potential effects of instream recreation, dredging, instream barriers, and water quantity alterations on *E. fonticola* populations. In addition, site fidelity and movement information for a narrowly distributed *Etheostoma* will provide further opportunity to assess relationships between instream movement and distributional ranges of small-bodied *Etheostoma*.

## METHODS

The headwaters of the Comal River are located in central Texas along the Balcones Fault Zone of the Edwards Plateau in a highly urbanized watershed. As with many Edwards Plateau rivers, base flow is supported by groundwater discharge from the Edwards Aquifer (Comal Springs) and has constant chemical and physical environmental conditions year round (Groeger et al. 1997). Instream damming regulates stream discharge and creates Landa Lake at the headwaters of the Comal River. Discharge from this impoundment enters either the old (former river channel) or new channel (constructed channel) through a head gate. The 2.5-km-old channel is the less anthropogenically altered section of the Comal River; stream width ranges from 10 to 15 m and maximum depth is 1.5 m. Site fidelity and movement were assessed in a 200-m reach of the old channel (29°42'39.66''W, 98°07'40.52''N) within a 1.5-km section of the old channel bounded on each end by road crossings with concrete culverts. Therefore, Fountain Darter movements are restricted to a 1.5-km section of stream.

The old channel reach of the Comal River was selected because the area supports little recreational activity and contains several vegetation types and a single geomorphic unit (run), which is typical *E. fonticola* habitat within the Comal and San Marcos rivers. Mark–recapture methods were used to evaluate site fidelity and movement. The 200-m reach was divided into three sections: a 100-m core section for marking and searching, and 50-m upper and lower sections for searching only. Dominant and subdominant aquatic vegetation were quantified in the area before the start of the study. Aquatic vegetation types were *Hygrophila polysperma* and *Ludwigia repens* (combined as one vegetation type based on similar growth forms and referred to as *H. polysperma* herein), *Riccia fluitans*, and filamentous algae *Rhizoclonium*. *Hygrophila polysperma* is a rooted macrophyte that extends through the water column, whereas *R. fluitans* and filamentous algae growth extends only a few centimeters above the substrate.

When available, four replicates (20 m<sup>2</sup>) of each vegetation type (*H. polysperma*, *R. fluitans*, filamentous algae, and mixed stands [*H. polysperma* with *R. fluitans*]) were selected in the 100-m core reach for sampling, and two replicates of each vegetation type were selected and sampled in the 50-m upstream and downstream reaches. Replicates were randomly selected at the beginning of the study if more than four replicates were available. Nonvegetated areas were not selected as replicates, because *E. fonticola* infrequently occurs in habitats lacking vegetation (Schenck and Whiteside 1976; Linam 1993). The midpoint of each replicate was established through GIS methods using a Trimble GeoXT (Trimble, Sunnyvale, California) to maintain a permanent record of replicate locations and obtain distances between pairs of replicates. Replicates were subdivided into multiple 5-m<sup>2</sup> quadrats. Each quadrat was sampled once with a drop net (2-m<sup>2</sup> frame with 1-mm mesh extending throughout the water column) for a maximum of four drop nets (8 m<sup>2</sup>) sampled in a 20-m<sup>2</sup> replicate. Replicates were consistently placed in the study reach, whereas quadrats within a replicate were randomly selected during each sampling event. The area covered by drop net was repeatedly swept with dip nets until no additional darters were captured after three successive attempts. At each quadrat, depth (cm), instantaneous flow (cm/s), pH, water temperature (°C) and dissolved oxygen (mg/L) were measured.

From August 2008 to June 2009, nine field collections were made among three seasonal units (summer–fall: August–October, winter: December–February, spring–summer: April–June). During the final sampling event, a seine survey was completed within the remaining 1.5-km section of the old channel to document darters that might have dispersed outside of the 200-m reach. For all collections excluding the final sampling event, *E. fonticola* were anesthetized in a 60-mg/L solution of tricaine methanesulfonate (Finquel, Argent Chemical Laboratories, Redmond, Washington). *Etheostoma fonticola* were sexed and TL (mm) was measured. Darters > 20 mm TL were marked with a unique batch mark to indicate time and location (replicate) of collection. Fish were marked with visible implant elastomer (VIE; Northwest Marine Technology, Shaw Island,

Washington) using a 0.3-cm<sup>3</sup> insulin syringe with a 29-gauge needle. The VIE mark has high retention in this species and the method has no observed effects on survival and growth in a laboratory study (Phillips and Fries 2009). To reduce potential stress on individual fish, only experienced personnel were used to mark wild fish in the field. To uniquely identify each batch of darters, the VIE mark was placed according to a combination of location on the fish and VIE color. Two marks were injected into each fish into two of five body locations (proximal base of left and right anterior dorsal fin, left and right ventral muscle tissue, and caudal peduncle) and with one or two of four possible color combinations. Darters were held in fresh river water until they recovered from the anesthetic and then were released in the sampling replicate from where they were captured.

Movement was measured as the distance (in meters) between midpoints of replicates where the darter was initially captured and the replicate where the darter was later recaptured. Individuals recaptured in the same replicate as the initial capture were classified as nonmovers and assigned a movement distance of 0 m. To assess directional bias in movement, upstream movements were assigned positive values, whereas downstream movements were assigned negative values. Mean distance moved was calculated for all fish with respect to direction of movement with and without nonmovers. To assess site fidelity, mean distance moved by recaptured fish was determined as the absolute value of distance moved (1) for all fish, (2) only fish classified as movers, and (3) with respect to direction including nonmovers.

Fidelity to the site of initial capture was assessed by comparing the mean distance moved by recaptured fish with the mean observable distance. Mean observable distance was defined as the mean distance between all pairs of replicates in the core 100-m section. One criticism of mark–recapture studies is that bias is introduced to the analysis by a study design in which shorter movement distances are sampled with greater frequency than longer distances (Albanese et al. 2003). This was evident in this study where 23% of pairs of sampling replicates were <10 m distant, whereas only 3% were >90 m. Therefore, randomization tests were used to compare the mean of the distribution of observable movement distances with the mean of the distribution of distances moved by recaptured fish. By considering only the frequency of observable distances, the bias introduced through study design was compensated in the analysis (Roberts et al. 2008).

All statistical tests were analyzed with the program R (version 2.9.1; R Development Core Team 2005). Estimate of directional bias in movement was assessed through a *t*-test of a single mean (Turchin 1998). Chi-square goodness of fit was used to test for differences in effort among vegetation types, vegetation type of initial capture and recapture, and sex ratio.

Logistic regression and corresponding Z-tests were used to identify factors associated with movement. Independent variables season, sex, body size (TL), and time elapsed between marking and recapture were examined. The dependent variable

for all models was the probability of an individual leaving the patch of initial capture. Models for comparison were built by combining the four independent variables and a null model for a total of 16 candidate models. Akaike's information criterion corrected for small sample size ( $AIC_c$ ) was used to evaluate models. Difference in  $AIC_c$  ( $\Delta AIC_c$ ) values was used as a measure of support for each model relative to the best model from the available data. Models with a  $\Delta AIC_c < 2$  are considered to have substantial support, whereas models with a  $\Delta AIC_c > 7$  are generally thought to have very little support and models have essentially no support when  $\Delta AIC_c > 10$  (Burnham and Anderson 2002). The model with the minimum  $AIC_c$  was interpreted for the influence of independent variables, which appeared in this model as the probability of an individual leaving the replicate of initial capture.

## RESULTS

A total of 434 quadrats were sampled in the available habitats. *Riccia fluitans* and *H. polysperma* were the most commonly sampled (28% each), followed by mixed stands (24%), and algae (21%). Availability of each vegetation type varied by season (ranges: 25–31% for *H. polysperma*, 26–30% for *R. fluitans*, 22–28% for mixed stands, and 15–24% for algae) and less algae and *R. fluitans* were available in winter and spring–summer, but effort among vegetation types did not differ (across seasons:  $\chi^2_3 = 7.0$ ,  $P = 0.07$ ; within seasons:  $\chi^2_{11} = 12.8$ ,  $P = 0.31$ ). Variation in available habitat within the study reach was consistent with typical seasonal trends in vegetation. Water depth was  $77 \pm 28$  cm (mean  $\pm$  SD) among habitats and ranged from  $51 \pm 24$  cm in algal habitats to  $102 \pm 20$  cm in *R. fluitans* habitats. Current velocity was  $7 \pm 6$  cm/s and ranged from  $3 \pm 2$  cm/s in algal habitats to  $12 \pm 7$  cm/s in *H. polysperma* habitats. Otherwise, abiotic conditions (i.e., dissolved oxygen, pH, and water temperature) varied little among habitats and through time. Water temperature was  $23.5^\circ\text{C} \pm 1.3^\circ\text{C}$ , pH was  $7.2 \pm 0.2$ , and dissolved oxygen content was  $8.3 \pm 1.8$  mg/L.

A total of 1,103 *E. fonticola* were captured and released. An additional 150 fish (lengths not taken; no marked fish found) were captured with seines within the remaining 1.5-km section during the final sampling event. Among the 1,103 captured with drop nets, 56 fish were captured during the final sampling event, measured, and their sex determined, but they were not marked. *Etheostoma fonticola*  $\leq 20$  mm TL ( $N = 105$ ) were released without marking: 68% were captured during spring–summer, 31% were captured in summer–fall, and 1% was captured in winter. *Etheostoma fonticola*  $> 20$  mm in TL ( $N = 942$ ) were captured, marked, and released from all vegetation types. Mortality due to anesthesia, handling, and marking prior to recovery was  $< 1\%$  ( $N = 7$ ). Length of darters  $> 20$  mm TL was  $29 \pm 3$  mm (mean  $\pm$  SD;  $N = 998$ ). Sex ratio did not differ ( $\chi^2_1 = 0.02$ ,  $P = 0.49$ ) from 1:1. The highest percentages of *E. fonticola* marked were captured and released in *R. fluitans* (44%) and algae (39%), followed by mixed stands (13%), and *H. polysperma*

(4%). *Etheostoma fonticola* density was  $1.3 \pm 0.9$  fish/m<sup>2</sup> and ranged from  $0.3 \pm 0.1$  fish/m<sup>2</sup> in *H. polysperma* to  $2.2 \pm 1.0$  fish/m<sup>2</sup> in algae.

Among the 942 marked *E. fonticola*, 8.7% ( $N = 82$ ) were recaptured with the highest percentages collected in algae (52%) and *R. fluitans* (32%), followed by mixed stands (15%), and *H. polysperma* (1%). Proportions of darters captured in each vegetation type differed between initial capture and recapture events when pooled across season ( $\chi^2_3 = 11.7$ ,  $P < 0.01$ ) but did not differ within season ( $\chi^2_0 = 14.9$ ,  $P = 0.09$ ). Among recaptured darters, 49% ( $N = 40$ ) were nonmovers, all of which were initially captured and recaptured in algae or *R. fluitans*. Of all recaptured darters 51% ( $N = 42$ ) moved from the site of initial capture. Ten individuals moved from algae or *R. fluitans* to another replicate of algae or *R. fluitans*. Thirty-two individuals moved into a vegetation type different from that where they were initially captured; 50% moved into algae, 34% into mixed stands, 13% moving into *R. fluitans*, and 3% into *H. polysperma*.

Distance of recaptured *E. fonticola* movement ( $N = 82$ ), incorporating the direction of movement, was  $6 \pm 19$  m (mean  $\pm$  SD) upstream and  $12 \pm 25$  m upstream when nonmovers were excluded. Movement was biased in an upstream direction ( $t = 2.90$ ,  $df = 81$ ,  $P < 0.01$ ) with 81% of darters classified as movers directed upstream (Figure 1). Independent of direction, distance of *E. fonticola* movement was  $10 \pm 17$  m for all recaptured fish or  $20 \pm 18$  m when nonmovers were excluded. The maximum distance moved by an individual was 95 m over a 26-d interval. Distances of *E. fonticola* movement among all fish, movers only, and upstream or downstream movers were less than the mean observable movement. Observable movement distance, which is the mean distance between all pairs of replicates in the core 100-m section, was  $35 \pm 27$  m and was greater than

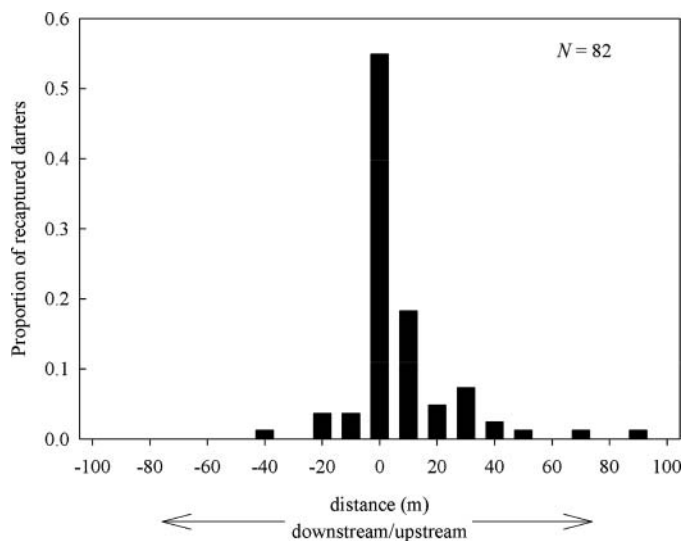


FIGURE 1. Frequency distribution of movement distances by *E. fonticola* in a 200-m stream section of the Comal River (Comal County), Texas, during a 1-year period.

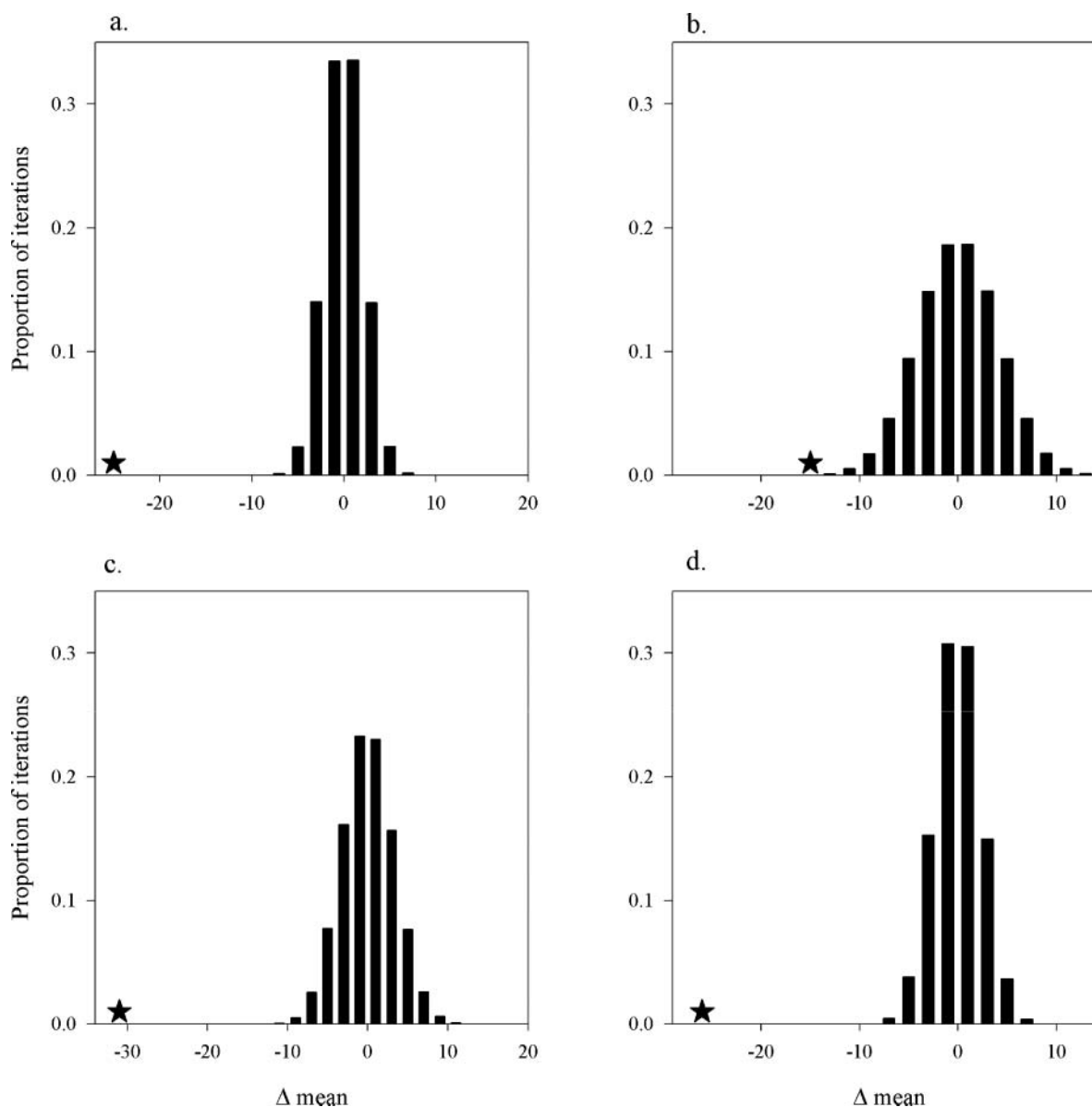


FIGURE 2. Outcome of randomization tests to assess site fidelity in *E. fonticola*. Frequency distribution of the difference between the mean observable distance ( $\Delta$  mean) and the 99,999 sample iterations from the randomization tests for (a) movers and nonmovers, (b) movers only, (c) downstream movers and nonmovers, and (d) upstream movers and nonmovers. Observed distances from recaptured individuals are designated by a star.

mean distance of *E. fonticola* movement of all recaptured fish ( $10 \pm 17$  m [mean  $\pm$  SD],  $P < 0.01$ ,  $N = 82$ ) and movers only ( $20 \pm 18$  m,  $P < 0.01$ ,  $N = 42$ ), upstream movers and nonmovers ( $9 \pm 16$  m,  $P < 0.01$ ,  $N = 74$ ), and downstream movers and nonmovers ( $4 \pm 10$  m,  $P < 0.01$ ,  $N = 48$ ; Figure 2).

Probability of *E. fonticola* movement was influenced by both season and TL (Figure 3; Table 1). The probability of an individual moving from the point of initial capture was 4.1 times greater in winter ( $Z = 2.5$ ,  $df = 77$ ,  $P = 0.01$ ) and 2.3 times greater in spring–summer ( $Z = 0.8$ ,  $df = 77$ ,  $P = 0.41$ ) as opposed to summer–fall (Table 2). The proportion of individuals classified as movers was 36% in summer–fall, 72% in winter,

and 55% in spring–summer. Probability of a darter moving from the replicate of initial capture was 1.2 times greater with every increase of 1 mm in TL ( $Z = 1.9$ ,  $df = 77$ ,  $P = 0.06$ ), and smaller fish ( $< 30$  mm) were classified as movers (32%,  $N = 31$ ) less frequently than larger fish ( $\geq 30$  mm; 64%,  $N = 50$ ).

## DISCUSSION

*Etheostoma fonticola* exhibited high site fidelity, moving on average  $10 \pm 17$  m (mean  $\pm$  SD) throughout the year during a stable hydrological regime (mean daily discharge,  $7.7$  m<sup>3</sup>/s; range,  $4.7$ – $8.7$  m<sup>3</sup>/s; USGS Station 08168913). Site fidelity

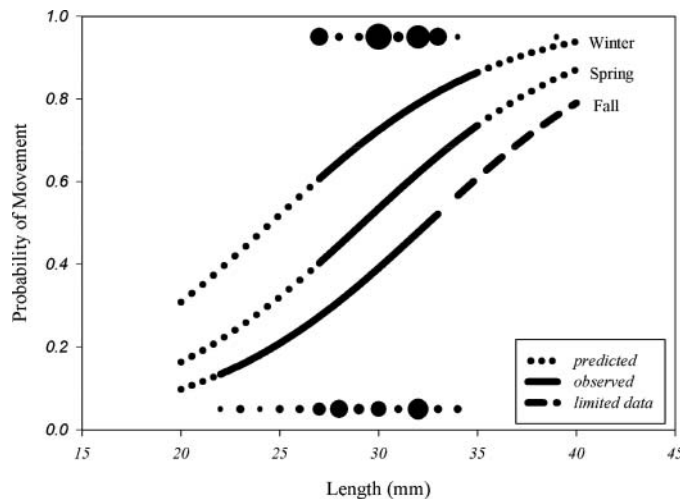


FIGURE 3. Logistic regression model of the probability of *E. fonticola* leaving the location of initial capture based on fish TL and season. Diameters of black circles represent the number of observed individuals per length, ranging from 1 (smallest circle) to 12 (largest circle), and indicates the relative number of the total observations used to develop the model. Black circles on the upper margin of the graph represent individuals that left the location of initial capture and those on the lower margin of the graph represent individuals that were found in the same location of initial capture.

TABLE 1. Candidate logistic regression models of *E. fonticola* movement. Models listed with predictors, number of parameters estimated ( $K$ ), log-likelihood, and ranked by Akaike information criteria corrected for small sample size ( $AIC_c$ ). Interpreted model is designated by an asterisk (\*).

Model predictors	$K$	Log-likelihood	$AIC_c$	$\Delta AIC_c$	Akaike weight
Length, season	4	-48.76	106.05	0.00	0.18*
Length, sex, season	5	-47.62	106.05	0.00	0.18
Sex, season	4	-49.19	106.90	0.85	0.12
Length, sex, time	4	-49.50	107.52	1.48	0.08
Season	3	-50.70	107.71	1.66	0.08
Length, time	3	-50.93	108.16	2.12	0.06
Length	2	-52.06	108.28	2.23	0.06
Length, time, season	5	-48.76	108.32	2.27	0.06
Length, sex, time, season	6	-47.62	108.38	2.33	0.06
Sex, time, season	5	-49.16	109.12	3.08	0.04
Length, sex	4	-50.63	109.79	3.75	0.03
Time, season	4	-50.67	109.87	3.83	0.03
Sex, time	3	-51.78	109.88	3.83	0.03
Time	2	-53.75	111.65	5.60	0.01
Sex	2	-54.05	112.26	6.22	0.01
Null	1	-56.09	114.23	8.18	0.00

TABLE 2. Summary of the logistic regression model selected by Akaike information criteria corrected for small sample size ( $AIC_c$ ) for *E. fonticola* movement: predictors ( $\beta$ ), regression coefficients (estimate), SD of estimate, Z-value, and P-value.

$\beta$	Estimate	SD	Z-value	P-value
Intercept	-5.76	2.80	-2.06	0.04
TL	0.18	0.09	1.87	0.06
Spring	0.58	0.70	0.83	0.41
Winter	1.41	0.56	2.50	0.01
Null deviance: 112.18 on 80 df				
Residual deviance: 97.52 on 77 df				

was most notable in areas with low growing aquatic vegetation (i.e., algae or *R. fluitans*). Distance of movement was  $20 \pm 18$  m among fish that moved from the initial area of capture (51%). Movement was most often towards areas with low growing aquatic vegetation (69%), more frequently in an upstream direction (81%), in winter and spring–summer seasons (>55%), and among larger fish (>30 mm TL). *Etheostoma fonticola* movement generally conformed to our initial predictions. As a small-bodied darter with preference for slackwater habitat and a narrow distribution, mean movement of the *E. fonticola* was considerably less than those reported for widely distributed and narrowly distributed, swift-water darters (122–181 m; Roberts and Angermeier 2007). As predicted, site fidelity was high, but *E. fonticola* moved more often (51%) from the initial area of capture than other slow-water darters, such as *E. cragini* (<20% moved from initial area of capture; Labbe and Fausch 2000) and *E. nigrum* (3%; Mundahl and Ingersoll 1983). The percentage of *E. fonticola* moving upstream was similar to those reported for both widely and narrowly distributed darters (73–86%; Roberts and Angermeier 2007).

Our prediction of high site fidelity during peak periods of reproduction (Scalet 1973; Mundahl and Ingersoll 1983) was not supported in this study. *Etheostoma fonticola* spawn year round but greater reproductive effort occurs during winter and summer (Schenck and Whiteside 1977). Movement among *E. fonticola* was highest among larger individuals and during their reported peak reproductive efforts, suggesting that movement increases and therefore site fidelity decreases during peak reproductive seasons as *E. fonticola* search for mates and suitable spawning areas. We attributed high site fidelity to the quality of available habitat that meets their year-round needs and as well as their needs during peak reproductive efforts. Site fidelity among benthic fishes is positively associated with habitat quality (Albanese et al. 2004; Roberts and Angermeier 2007; Breen et al. 2009) and decreases when habitat quality is altered (Gowan and Fausch 2002; Roberts and Angermeier 2007). *Etheostoma fonticola* are often associated with low-growing aquatic vegetation in the San Marcos and Comal rivers (Schenck and Whiteside 1976; Linam et al. 1993; Alexander and Phillips 2012). They opportunistically feed on drifting and pelagic

copepods and cladocerans, as well as benthic amphipods, dipterans, and ephemeropterans commonly found above and in attached vegetation (Bergin 1996), and lay adhesive eggs on vegetation or on bare substrates (Schenck and Whiteside 1977; Brandt et al. 1993; Phillips et al. 2011). Consequently, preference for low-growing aquatic vegetation, such as algae and *R. fluitans*, probably optimizes a balance among being a benthic invertivore lacking a swim bladder, consuming drifting and benthic prey, and having a phytolithophil reproductive strategy while avoiding piscivorous predators.

Maximum distance moved was 95 m within 26 d, and 7% of *E. fonticola* moved farther than the mean observable distance (35 m). Maximum distance moved by *E. fonticola* is similar to those reported for widely distributed (100–500 m) and narrowly distributed darters (185–250 m: Mundahl and Ingersoll 1983; Roberts and Angermeier 2007), less than those reported for swift-water, riffle-associated darters (250–500 m), and similar to those reported for slackwater darters or darters observed in slackwater habitats (100–200 m), excluding migratory darters (*E. boschungii* move up to 3 km: Boschung and Nieland 1986). Percentages of darters moving >33 m within a year range from 3% to 13% (Mundahl and Ingersoll 1983; Roberts and Angermeier 2007). The tendency for a small proportion of individuals moving greater distances than conspecifics is common among stream fishes, including centrarchids, cottids, cyprinids, and percids (Hill and Grossman 1987; Smithson and Johnston 1999; Roberts et al. 2008). Long-distance movement observed in some individuals is probably based on genetics (e.g., boldness: Fraser et al. 2001) and could be essential to dispersion and colonization abilities of a population (Turchin 1998). More mobile individuals disperse at faster rates (Skalski and Gilliam 2000) and are probably the first to reach newly available or defaunated habitats (Scheurer et al. 2003) and areas of refugia during periods of duress (Labbe and Fausch 2000). Potomac Sculpin *Cottus girardi*, a species with high site fidelity, repopulated experimentally defaunated areas rapidly, probably as a result of a small percentage of a large population making longer movements (Hudy and Shiflet 2009). Consequently, maintaining conduits for movement is not only important for migratory species (i.e., Mountain Mullet *Agonostomus monticola*, freshwater eels, numerous cyprinids: Lee 1980; McDowall 1988; Skov 2008) but also for fishes that exhibit high site fidelity (Roberts and Angermeier 2007; Breen et al. 2009).

The Comal and the upper San Marcos rivers are located within the third-most populated area of Texas (Austin–San Antonio corridor) and are identified as critical habitat for *E. fonticola* and several other federally listed taxa (USFWS 1980). Headwaters of both rivers emerge within urbanized watersheds and have undergone extensive instream modifications, including channelization, construction of low-head dams, dredging, and water quantity alterations (Sanborn 1944; Kimmel 2006). Currently, the rivers are popular summertime destinations for waders, swimmers, and for those engaging in other types of

water recreational activities. Instream uses and modifications pose potential additional concerns for species with high site fidelity, such as the *E. fonticola*. A habitat conservation plan (Thornton 1993) recently was accepted by the U.S. Fish and Wildlife Service that will request the incidental take of federally listed species within the Comal River and San Marcos River systems while minimizing and mitigating effects of river use by local government entities. Local government entities propose a number of measures and presumably recovery efforts to mitigate and minimize effects of river use on listed species, including flow management of the old channel, nonnative plant and animal removal, native aquatic plant reintroductions, management of public recreation use, and sediment removal. Quantification of Fountain Darter site fidelity and movement will inform mitigation and minimization efforts by providing predictions on how the Fountain Darter will respond to alterations of their current habitat (i.e., removal of nonnative vegetation and sediment, water level fluctuations during flow management), disruption of habitats by recreational use, and recolonization expectations of native vegetation reintroductions. Another implication of the quantification of Fountain Darter movement is the effect that low-head dams and culverts have on fragmentation of the Fountain Darter population and the impedance of a few more mobile individuals on gene flow and genetic diversity. This issue is not addressed in the habitat conservation plan but is necessary given the results of this study. This study quantified *E. fonticola* site fidelity and movement during a base flow hydrological condition that was slightly less than average. Quantifying site fidelity, movement, and other related life history characteristics (e.g., reproductive success and feeding) under various hydrological regimes (i.e., subsistence flows, higher base flows, high flow pulses) and levels of recreational use will provide a better model of community responses to natural and anthropogenic environmental influences.

As a representative of the small-bodied and narrowly distributed etheostomids, the proportion of *E. fonticola* with high site fidelity and the maximum distance moved was not noticeably different from that of widely distributed etheostomids. As such, movement potential and maximum movement do not satisfactorily explain why some darters are more widely distributed than others. However, differences in the upper range of maximum distance moved differed between slackwater-associated (250 m) and swift-water-associated (500 m) darters. These differences may be sufficient to explain observed patterns in localized extirpation and subsequent recolonization after periods of no flow to low flows or high flow pulses. *Etheostoma fonticola* in the Comal River were considered extirpated in 1973, which was probably attributed to a rotenone treatment in the headwaters in 1951, low-flow conditions in 1954, a catastrophic flood in 1972, or combination of the three events (Schenck and Whiteside 1976). High site fidelity and restricted movement of *E. fonticola* would predictably slow recolonization after these events. In contrast, population densities of the swift-water-associated *E. grahami* were unaffected by a catastrophic flood (Watson



2006). Understanding the role restricted movement plays on recolonization of suitable habitat in light of anthropogenic fragmentation of populations is one of the necessary next steps towards development of a conservation plan for this and other imperiled etheostomids.

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